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AN EXAMINATION OF THE STRIP CENSUS METHOD FOR ESTIMATING ANIMAL POPULATIONS[1]

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A method for estimating populations of grouse, commonly known as the strip census method, or the "King method," was described by Leopold (1933) from unpublished work of R. T. King. The present paper examines an apparently erroneous assumption inherent in this method as ordinarily used. The many biological considerations which determine the method's usefulness in censusing any particular species are here largely ignored. The discussion assumes that the method is being applied where biologically suitable.

In the original description by Leopold (1933), the method was applied to censusing brooding ruffed grouse. Among various applications of the method have been those of Fisher (1939) and Frank (1946) working with ruffed grouse, Erickson (1940) and Krefting and Fletcher (1941) working with white-tailed deer, Webb (1942) with snowshoe hares, and DeBoer (1947) in a forest tally of dead deer. Kendeigh (1944) mentions use of an apparently identical method with a number of species of birds. Colquhoun and Morley (1941) describe a method which is similar except that, instead of computing average flushing distance, the farthest limit of the "band of greatest density" in a distribution of observed flushing distances is determined by inspection.

As the census method is now used, the observer walks along a predetermined line and records the number of animals and the distances from himself to the animals flushed. The average flushing distance is computed. This average distance is assumed to be one-half the "effective width" of a strip covered by the observer. The total number of animals flushed is then assumed to equal the population of a strip of "effective width," those animals flushing at a distance greater than the "effective" distance, compensating for those which were present at a lesser distance from the observer and did not flush. From the estimated population of this strip of known length and "effective" width, the investigator computes population density per unit area. Various computing formulae have been suggested; that given by Fisher (1939) being:

$$P = \frac{AZ}{XY} \qquad (1)$$

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where P = the estimated total population of the area censused
A = total area of the tract
Z = total number of grouse actually observed
X = total distance walked by the observer
Y = twice the average distance from the observer to the bird when flushed.

The real contribution of Professor King lies in pointing out that flushing behavior of animals in the presence of an observer may furnish a clue as to whether many or few animals are being missed (not flushed). The problem here discussed concerns use of flushing behavior in relating the number flushed to an estimate of total number present.

FUNDAMENTAL ASSUMPTIONS

The method of estimating population under discussion is based upon certain fundamental assumptions, the chief of which appear to be:

1. That in a population animals vary with regard to distance at which they will flush or be seen upon the approach of an observer.
2. That the various classifications of animals (with regard to flushing distance) are scattered about over the study area in a random fashion, at least relative to the path of the observer.
3. That the average of the flushing distances observed by the investigator is a good estimate of the true average of all flushing distances throughout the population being studied.

The first assumption, that not all animals flush at the same distance, seems confirmed by any set of field data (see Tables 1, 2 and 3). In the present discussion the term "flushing distance" is considered to characterize the behavior of an individual animal only at the moment of the observer's closest approach. When this distance of closest approach equals the flushing distance, the animal is flushed, otherwise the observer's distance is always greater than the flushing distance. Since flushing distance is an almost instantaneous measurement of behavior, it is not necessary to assume that each animal maintains the same flushing distance throughout the census period, although it seems necessary that the population as a whole keep the same frequency distribution of flushing distances. What determines the flushing distance, whether the important factors are external or internal to the animal, is not well known. The type of surrounding cover seems important, for example Frank (1946) shows differing values for observed average flushing distance of ruffed grouse in various cover types. Other possible factors governing this type of behavior appear not to have been investigated.

The second assumption is that there exists no significant tendency for animals flushing at any particular distance to occur near the observer's path in any smaller, or in any greater, numbers than are found throughout the entire area. Because of the importance of cover, the sampling of the study area must be without bias. Several observers have used compass lines, spaced in a manner assumed to sample adequately the cover types present. Fisher (1939) used this plan and then, following a modification credited by him to M. C. Wakeman and J. H. Stephenson of the Michigan Department of Con-

servation, estimated separately the population within each cover type present. An uncorrected error is introduced by any directional movement of animals in relation to the observer's path. For example, certain carnivores appear to avoid an observer so successfully that "flushing distance" must be considered greater than the range of visibility. Another source of error is any tendency for animals to "drive," that is, to move down the line of travel ahead of the observer after being flushed, thus increasing the apparent population density. Finally, an observer may fail to sight animals which have been flushed.

The third assumption, that the observed average flushing distance is a good estimate of the true average flushing distance in the population, is here shown to be incorrect. The difference between the two average values, and the difference between resulting population estimates may be stated in mathematical terms, and such a comparison will be found in the appendix of this paper.

ILLUSTRATION OF FALLACY IN THIRD ASSUMPTION

In order to demonstrate the fallacy of the third assumption without recourse to mathematical symbols, an example is worked out. These imaginary census figures are extreme, but designed to illustrate the error present. Actual field examples will be presented later.

In order to simplify this example, imagine that the observer travels once from end to end of the study area. The population estimate for the entire area will then bear the same relationship to the population of the sampled strip as width of area bears to width of strip. Assume that the study area is 1,000 yards wide and contains 1,375 animals, composed of 1,250 animals which will flush at a distance of 2 yards, and 125 animals which will flush at 20 yards. The true average flushing distance in this population is, therefore, 3.64 yards.

In passing through the area once, the observer will flush a certain proportion of each of the two classes of animals. Under ideal conditions, he will flush 4/1,000 of the 1,250 animals which flush at 2 yards, or 5 animals, and of the 125 flushing at 20 yards, he will flush 40/1,000, or, again, 5 animals. The observed average flushing distance is 11 yards, a value considerably above the true population value of 3.64 yards.

Using the observed average flushing distance to estimate the population, it is assumed that each strip 22 yards wide (twice the average flushing distance) will contain 10 animals, and there being 45.4 such strips, the population is estimated at 454 animals, or only about one-third of the true value.

If each class with regard to flushing distance is computed separately, this error is avoided. If each strip 4 yards wide (2 yards either side) contains 5 animals flushing at 2-yards distance, the area contains 250 such strips, or 1,250 animals of this class. At the same time, each strip 40 yards wide contains 5 animals flushing at 20 yards, and with 25 such strips there are 125 animals of this class on the area. The sum, 1,375, correctly estimates the total population.

The same example may be considered

from the point of view of the investigator using an average flushing distance in estimating numbers present. If only the 5 animals flushing at 2 yards are considered, the observed average distance is 2 yards and the population estimate is 1,250. However, inclusion of the 5 records of 20-yards flushing distance, while it *increases* by 100 per cent the number of birds observed, *reduces* by 64 per cent the population estimate.

It seems clear that in this example the average of the observed flushing distances is not a good estimate of the true population average flushing distance, and, therefore, should not be used in computing a population estimate. Each class of animal, according to flushing distance, may be estimated separately, and the sum of these subpopulations will furnish an estimate of the total population.

COMPUTING FORMULA

The following formula is based upon the separate estimation of the various classes of animals with regard to flushing distance, as explained in the appendix. To reduce labor of computation the quantities constant for any one census are grouped ($c/2L$). This working formula estimates population per unit area:

$$N_T = \frac{c}{2L}\left(\frac{F_1}{d_1} + \frac{F_2}{d_2} + \frac{F_3}{d_3} + \cdots + \frac{F_n}{d_n}\right) \quad (2)$$

where

N_T = estimate of total population per unit area

L = length of observer's path, or census strip

$d_1, d_2, d_3, \cdots d_n$ = the various flushing distances observed

$F_1, F_2, F_3, \cdots F_n$ = numbers of animals observed to flush at the corresponding flushing distances

c = conversion factor where units are not comparable, for example, $c = 43{,}560$ when L and values of d are stated in feet and N_T is desired in animals per acre.

When the population of the entire study area is to be estimated, the above per-unit-area estimate must be multiplied by the area.

Estimates of population made by this formula are, of course, still subject to errors of random sampling and to any systematic errors from mistakes in the basic assumptions. The errors of random sampling appear to be large, judging from published figures of Fisher (1939) and Frank (1946), as well as unpublished data of the Michigan Department of Conservation examined by the present author. Considerable differences occur between consecutive sets of data which pertain to the same area and presumably to the same population. Systematic errors, such as result when animals move out of the observer's path, are of unknown magnitude, and might invalidate any strip census technique.

The formula suggested above does, however, correct the systematic error inherent in the ordinary method of strip census, where population estimates based upon the observed average flushing distance tend consistently to underestimate the population. As shown in the appendix, the importance of this error varies with the ratio of the observed to the true average flushing distance.

FIELD EXAMPLES

In order to illustrate further the use

of the method, three representative sets of unpublished field data have been drawn from two sources. The first example pertains to a pheasant drive conducted under the direction of Professor B. T. Ostenson, to whom appreciation is expressed for the use of these data. The other two examples, relating to ruffed grouse, are from the files of the Game Division of the Michigan Department of Conservation. Appreciation is expressed to Mr. H. D. Ruhl, of the Game Division, for permission to use these unpublished data for purposes of illustration.

The pheasant drive was conducted in December, 1942 on part of the Michigan State College Farm, East Lansing, Michigan. Seventy flushing distances were recorded as estimated by a number of reliable observers among the drivers, and these data are assembled in Table 1. The great variation to be seen in these flushing distances is probably attributable to the wide variety of types of cover found on the study area, ranging from barren stubble fields to dense grass and shrub cover. Since the drivers were spaced about 180 feet apart, a certain number of birds were not flushed and, hence, were not counted. The fundamental idea of the King method was adapted to aid in estimating the proportion of birds present which were not flushed. The formula (2), as given, does not cover all aspects of the drive type of census, but the basic reasoning is the same in the following discussion.

TABLE 1.—DATA RELATING TO PHEASANT DRIVE OF DECEMBER, 1942, ON THE MICHIGAN STATE COLLEGE FARM, EAST LANSING, MICHIGAN

Flushing Distance in Feet	Pheasants Observed	Estimated Proportion Flushed of Those Present	Estimated Numbers Present on Observers' Strips
5	3	.06	50
10	4	.11	36
15	7	.17	41
20	4	.22	18
25	2	.28	7
30	11	.33	33
35	2	.39	5
45	5	.50	10
50	7	.56	12
60	8	.67	12
75	3	.83	4
90	4	1.00	4
100	2	1.00	2
120	2	1.00	2
150	2	1.00	2
180	2	1.00	2
300	1	1.00	1
450	1	1.00	1
Total	70		242

The theoretical proportion of birds seen out of the total number present is listed in Table 1 for each flushing distance. For any flushing distance less than 90 feet, this porportion is simply the ratio of twice the flushing distance to 180 feet. For example, of birds flushing at 45 feet, one-half should have been flushed. It is assumed that all birds inclined to flush at a distance greater than 90 feet were seen by the party. From these proportions of birds seen may be estimated the number of birds present in each class, on areas covered by the observers. For example, if it is assumed that half of the birds flushing at a 45-foot distance were seen, then the 5 birds seen represented a total of 10 birds present. The sum of the various classes may be used for computing the proportion seen of birds present. In the present example, 70 birds were flushed from an estimated 242 birds present in the areas sampled by the observers. This indicates that the total number of birds seen by the

entire party should be multiplied by a factor of 3.46 in order to account for birds not flushed.

On the other hand, if the average flushing distance of all birds observed (59.7 feet) is used in estimating the number not flushed, 66 per cent of the area is assumed to have been covered, and the same proportion of all birds present to have been sighted. By this reasoning, the total population was only 1.51 times as numerous as the birds observed.

The two remaining examples relate to ruffed grouse, data being gathered in the Pigeon River State Forest by members of the Michigan Department of Conservation. The particular area censused was described by Fisher (1939) as his "Area II." Field data relating to a total of 63 censuses made between January 2, 1940 and April 28, 1941 were made available to the present author. For purposes of comparison, these data have now been computed in two ways: first, assuming the observed average flushing distance to be half of the "effective width" of the strip covered by the observers; second, computing separately the number of birds inclined to flush at the various distances, in the manner recommended in the present paper. This second method of computation produces estimates invariably larger than those computed by use of the observed average flushing distance. This result is predictable from mathematical considerations, as shown in the appendix. The actual differences between estimates vary over a wide range, the largest difference being 68 per cent, and the smallest difference 2 per cent, of the larger estimate. The average of the 63 percentage differences is 30 per cent. From these 63 sets of field data, two sets have been chosen for detailed examination here. The first of these examples illustrates similar population estimates by the two methods of computation, while the second example illustrates divergent estimates.

Data for the first example were gathered on December 2, 1940. The field data are given in Table 2, with the values for the fraction F/d required in formula 2. In this census area, the total length of the observer's path is such that when the quantity $c/2L$ in formula 2 is equal to 31.45, the results are expressed as birds per square mile. Computation of the population estimate consists in summing the various values of the fraction F/d, and then multiplying this sum (0.91) by 31.45 according to formula 2. The resulting estimate is 29 birds per square mile.

TABLE 2.—FIELD DATA ON RUFFED GROUSE CENSUS OF DECEMBER 2, 1940, PIGEON RIVER STATE FOREST, PREVIOUSLY UNPUBLISHED DATA FROM THE FILES OF GAME DIVISION, MICHIGAN DEPARTMENT OF CONSERVATION

Flushing Distance in Yards (d)	Number of Grouse Flushed (F)	F/d	Estimated Population per Sqare Mile
10	1	.10	3
14	1	.07	2
18	1	.06	2
20	5	.25	8
22	2	.09	3
24	2	.08	3
26	5	.19	6
30	2	.07	2
Total	19	.91	29

On this day, the observed average flushing distance was 22.3 yards. If the "effective width" of the observer's path is then assumed to have been

44.6 yards, the population estimate is 27 birds per square mile. The results of the two methods of computation do not differ greatly in this case.

The estimated numbers of birds per square mile inclined to flush at the various distances are listed in the last column of Table 2. The average flushing distance throughout the total population may be estimated at 21.0 yards, not greatly different from the value of 22.3 yards for the birds actually observed, and the error from assuming that the two average flushing distances are the same is consequently not large.

The second example, where the estimates are different, uses data gathered on July 17, 1940. The field data are shown in Table 3 along with the computations previously described. The population estimated by the method here recommended is 208 birds per square mile. The observed average flushing distance was 13.1 yards, and an estimate of population using this average is 105 birds per square mile, a value only 51 per cent as large as by the first method. In this example, the average flushing distance throughout the population may be estimated at 6.6 yards, or only about one-half of the value of 13.1 yards observed. A large error arises here from the assumption that the observed flushing distances constituted a true sample of the behavior of the birds throughout the entire population.

TABLE 3.—FIELD DATA ON RUFFED GROUSE CENSUS OF JULY 17, 1940, PIGEON RIVER STATE FOREST, PREVIOUSLY UNPUBLISHED DATA FROM THE FILES OF GAME DIVISION, MICHIGAN DEPARTMENT OF CONSERVATION

Flushing Distance in Yards (d)	Number of Grouse Flushed (F)	F/d	Estimated Population per Square Mile
2	8	4.00	126
10	12	1.20	38
14	14	1.00	31
24	9	.38	12
30	1	.03	1
Total	44	6.61	208

TESTING FIELD DATA FOR CERTAIN ERRORS

If the assumptions basic to the use of the strip census technique are not met, errors are introduced. It may be possible to correct for some of these errors, or the use of the census technique may have to be abandoned. In either case, before reaching a decision, it seems necessary to compare the field data to the type of data to be expected in the absence of error. Breckenridge (1935) and Webb (1942) have considered separate aspects of error in a strip census, and their work will be discussed here.

Breckenridge (1935) working with small birds believes that a portion of the birds occurring on his line of traverse (a compass line) anticipate his course of travel, move through the vegetation, and flush at a short distance on either side. While he raises this question incidental to use of another census procedure, the point is important to the method here discussed. Such a movement would confute the assumption that animals are distributed at random in relation to the observer's path, and would introduce errors of unknown magnitude. Hence it is desirable to determine whether such a movement may be occurring.

Basis for a test seems to lie in the fact that, with no movement, animals flushing at any particular distance

should be equally numerous on strips of equal area. Thus any strip parallel to the observer's path and at a stated distance should contain a predictable proportion of the flushing observations of each class of animal. This proportion should equal the ratio of width of strip to flushing distance characterizing the class, except when considering a strip at the extreme distance of flushing of the class.

For example, consider with relation to the observer's path the distribution of an imaginary group of animals flushing at distances from 20 to 30 feet. About $\frac{1}{3}\frac{0}{5}$ of these may be expected on the two strips extending either side of the observer's path for 10 feet. The same proportion ($\frac{1}{3}\frac{0}{5}$) may be expected on the strips located between 10 and 20 feet from the path. The remainder of the observations, $\frac{5}{3}\frac{5}{5}$, may be expected on the strips between 20 and 30 feet. This outside strip will contain only about half as many observations as strips of equal area located nearer the path, since part of this outer strip extends to a distance greater than the flushing distance of some of the animals.

The number of observations expected upon any pair of strips may be computed as the sum of the proportions of each class to be expected on the strips. Continuing the imaginary example, upon the strips extending from 20 to 30 feet from the observer's path, on each side, may be expected $\frac{5}{3}\frac{5}{5}$ of all animals flushed at between 20 and 30 feet, $\frac{1}{3}\frac{0}{5}$ of animals flushed at between 30 and 40 feet, $\frac{1}{1}\frac{0}{5}$ of animals flushed at between 40 and 50 feet, and similar proportions of all other classes with regard to flushing distance. The sum of all such proportions will be the number expected upon the pair of strips and may be compared to the number actually seen. This proposed test requires field records of both flushing distance and distance of the animal from the observer's path. No such data are available to the author for use as an illustration.

Breckenridge uses an approximate test, by inspection, which is based upon the assumption that observations on strips closer to the investigator should be at least as numerous as those on more distant strips. When observations on nearer strips are significantly less than on distant strips, an outward movement is indicated. However, when observations are more equally distributed, such a test would fail to distinguish between the normal result of all flushing distances being equal and the effect of an outward movement.

Webb (1942) in censusing snowshoe hares has recorded both the distance from the observer to the animal when first seen, and the angle of the observation. This angle may be defined as the acute angle between the line of traverse of the observer and a line from the observer to the animal (angle POA in Figure 1). These "jumping angles" should vary between zero when the animal is on the line of traverse and 90 degrees when it is at the observer's extreme right or left hand. Webb appears to feel that too small a proportion of the animals are flushed at the larger jumping angles. As a correction, he suggests that the "average width of the strip on which the hares are seen" be computed; in other words, twice the average perpendicular distance from the line of traverse to the point of flushing.

The first question to be raised concerns the distribution of "jumping angles" to be expected, provided the observer sights every animal which is flushed. Inspection of Figure 1 indicates that the average of such angles will not be 45 degrees as might be casually imagined, but some lesser value. Figure 1 shows a series of 10 strips of equal width parallel to the observer's line of travel. If there is only one value of the flushing distance, equal in this case to the combined width of the 10 strips, then any animal within these 10 strips will be flushed, and none beyond this. Since the population is evenly distributed, there will be the same number of animals flushed on the inside strip between the angles of 0° and 5°44′ (sine equals 1/10) as are flushed on the farthest strip, between the angles of 64°9′ (sine equals 9/10) and 90° (sine equals 1). The same number of observations will be spread in the one case over a range of less than 6 degrees and in the other case over a range of about 26 degrees. In the intervening range of jumping angles the relationship varies between these extremes.

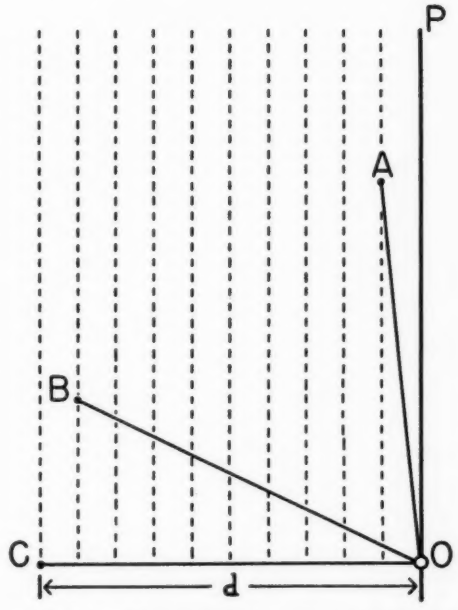

FIG. 1.—Diagrammatic representation of the distribution of angles of observation. The observer's path *OP* is shown with 10 parallel strips of equal population, with flushing distance *d* equal to the width of the 10 strips. There should be the same number of animals flushed on each strip, and therefore between the angles zero degrees and *AOP* should be the same number of observations as between the angles *BOP* and *COP*. Right-hand side of the diagram is omitted.

The average value of a series of angles distributed as illustrated in Figure 1 may be determined approximately from this figure as about 33°, or more exactly by a mathematical solution furnished to the author by Professor Leo Katz, as 32° 42′ 15.2″ (see appendix). Since this average value of the angle of observation does not depend upon the distance of the animal when it is flushed, it should be about the same for all distances, and therefore for an entire set of data. The six field values for the observed average "jumping angle" furnished by Webb in his 1942 paper fall surprisingly close to the theoretical value, being given as 32°47′, 33°58′, 31°46′, 31°45′, 35°41′, and 33°52′. It would seem, therefore, that the averages in Webb's data fall very close to those expected in the absence of the error which he suspects.

The average of the sines of a series of angles of observation should equal 0.5 under ideal conditions. This fact is obvious from Figure 1 since, for any one flushing distance, there are as many animals present on one of the parallel strips as on any other, and the sine of the angle is equal to the distance of

the animal from the observer's line of travel divided by the flushing distance. This fact offers at least an approximate means of testing whether a set of data may be subject to the error as suggested by Webb, or whether the departure may be attributed to chance. For example, as read from the text figure given by Webb, the sines of the angles of observation in that set of field data appear to average about 0.41, with a standard error of about 0.08. It appears, therefore, that the average of these sines does not depart significantly from 0.5.

If the data are found subject to a significant error of this type, it is probable that correction should be made by a system of weighting of observations at the various angles. A second observer, trailing the first and recording the animals missed by him, might furnish data for such a system. The correction offered by Webb, that the "average width of the strip on which the hares are seen," be used appears to have no logical relationship to the type of error which he has suggested. For example, if this correction is applied to data where the suspected error is absent, it simply doubles the population estimate.

SUMMARY

The method of strip census as ordinarily used assumes that flushing distances observed by the investigator constitute a good sample of the flushing distances of all animals throughout the population studied. Since this assumption appears to be incorrect, population estimates based upon observed average flushing distances are in error.

It is here suggested that the population of each class of animal with regard to flushing distance be estimated separately, the sum of these several subpopulation estimates being the estimate of total population. A formula is offered for use in this computation.

Two previously suggested sources of error, namely, the movement of animals out of the observer's path, and the failure of the observer to sight animals flushing to the right or left, are discussed as to type of field data to be expected.

A mathematical discussion of the problem is given in the appendix of this paper.

APPENDIX

Let a unit area contain a total population of animals, N_T, made up of a number of subpopulations, N_1, N_2, N_3, . . . , N_n, each of which is characterized by its own flushing distance, d_1, d_2, d_3, . . . , d_n, respectively. The arithmetic mean of flushing distances throughout the entire population is:

$$\frac{N_1d_1 + N_2d_2 + N_3d_3 + \cdots + N_nd_n}{N_1 + N_2 + N_3 + \cdots + N_n} \quad (3).$$

As an observer passes along a line of length L the animals which will be flushed at the distance d_1 will be those present on the strip of length L and width $2d_1$. The number flushed, designated F_1, will then be equal to $2d_1LN_1$ if all units used are comparable. A factor, c, must be included where units are not comparable, as when, for example, d_1 and L may be stated in feet, and N_1 in animals per acre, requiring c to equal 43,560. Thus the number flushed at d_1 will be:

$$F_1 = \frac{2d_1LN_1}{c} \quad (4),$$

and a similar relationship holds for each of the other classes of animals. The total of all animals flushed will be the sum of:

$$\frac{2d_1LN_1}{c} + \frac{2d_2LN_2}{c} + \frac{2d_3LN_3}{c} + \cdots + \frac{2d_nLN_n}{c}$$

or,

$$\frac{2L}{c}(N_1d_1 + N_2d_2 + N_3d_3 + \cdots + N_nd_n).$$

The area of a strip of length L and width equal to twice the *true* average flushing distance (formula 3), incorporating as before a constant (c) for conversion of units, would be:

$$\frac{2L}{c}\left(\frac{N_1d_1 + N_2d_2 + N_3d_3 + \cdots + N_nd_n}{N_1 + N_2 + N_3 + \cdots + N_n}\right).$$

If this strip is assumed to contain a population equal to all animals flushed the population per unit area becomes:

$$N_T = \frac{\frac{2L}{c}\left(N_1d_1+N_2d_2+N_3d_3+\cdots+N_nd_n\right)}{\frac{2L}{c}\left(\frac{N_1d_1+N_2d_2+N_3d_3+\cdots+N_nd_n}{N_1+N_2+N_3+\cdots+N_n}\right)},$$

or,

$$N_T = N_1 + N_2 + N_3 + \cdots + N_n$$

which is indeed the total population per unit area. Thus the population may be estimated from the number flushed, if the *true* average flushing distance is known.

However, the real average flushing distance is not apparent to the investigator, since he can record only the flushing distances of those animals which are seen. The *observed* average flushing distance, relating only to animals seen, will be:

$$\frac{\frac{2d_1LN_1}{c}d_1 + \frac{2d_2LN_2}{c}d_2 + \frac{2d_3LN_3}{c}d_3 + \cdots + \frac{2d_nLN_n}{c}d_n}{\frac{2d_1LN_1}{c} + \frac{2d_2LN_2}{c} + \frac{2d_3LN_3}{c} + \cdots + \frac{2d_nLN_n}{c}},$$

or,

$$\frac{N_1d_1^2 + N_2d_2^2 + N_3d_3^2 + \cdots + N_nd_n^2}{N_1d_1 + N_2d_2 + N_3d_3 + \cdots + N_nd_n} \quad (5).$$

If the total number of animals flushed is now credited to a strip of length L and width equal to twice the *observed* average flushing distance (formula 5, above), in the manner usual in the strip census method, the estimate of population per unit area becomes:

$$\frac{\frac{2L}{c}\left(N_1d_1+N_2d_2+N_3d_3+\cdots+N_nd_n\right)}{\frac{2L}{c}\left(\frac{N_1d_1^2+N_2d_2^2+N_3d_3^2+\cdots+N_nd_n^2}{N_1d_1+N_2d_2+N_3d_3+\cdots+N_nd_n}\right)},$$

or,

$$\frac{(N_1d_1+N_2d_2+N_3d_3+\cdots+N_nd_n)^2}{N_1d_1^2+N_2d_2^2+N_3d_3^2+\cdots+N_nd_n^2} \quad (6).$$

Where there is no variability in flushing distance, in other words, where all the values $d_1, d_2, d_3, \ldots, d_n$ are equal, the estimate above (formula 6) will equal the population, and the *observed* average flushing distance will equal the *true* average flushing distance. Under the more usual condition of variability in flushing distance, the population estimate given in formula 6 will be less than the actual population. The error may be identified in the following manner.

The various quantities may be rewritten in the more usual statistical notation, where X represents the flushing distance of an individual animal, and ΣX, for example, represents the summation of all such values throughout the entire population. Formula 6, then, is restated as:

$$\frac{(\sum X)^2}{\sum X^2}.$$

This population estimate by the usual method will be a certain proportion of the total number in the population (N), as follows,

$$\frac{(\sum X)^2}{N\sum X^2}.$$

This ratio also equals the true average flushing distance (formula 3) divided by the observed average flushing distance (formula 5). The difference between this ratio and unity will be the error of estimation, stated as a proportion of the population, as follows,

$$1 - \frac{(\sum X)^2}{N\sum X^2},$$

or,

$$\frac{N\sum X^2 - (\sum X)^2}{N\sum X^2}.$$

If both numerator and denominator of this fraction are divided by N^2, the value remains unchanged,

$$\frac{\frac{N\sum X^2 - (\sum X)^2}{N^2}}{\frac{N\sum X^2}{N^2}} \qquad (7).$$

Since the variance (V) in flushing distance throughout the entire population may be written as:

$$V = \frac{N\sum X^2 - (\sum X)^2}{N^2},$$

the expression (7) above may be stated as:

$$\frac{V}{\frac{\sum X^2}{N}} \qquad (8).$$

Thus, the estimate by the usual strip census method stands in the same ratio to the population number as the true average flushing distance bears to the observed average flushing distance, and the error stated as the proportional difference between the estimate and the population number is related directly to the variance in flushing distance, and inversely to the average squared flushing distance, as shown immediately above.

It is here recommended that the estimate of total population be attained by adding the separate estimates for each flushing distance observed. If F_1, the number flushed at d_1, is credited to a strip of length L and of width $2d_1$, the estimated population per unit area *of animals flushing at* d_1 will be:

$$N_1 = \frac{cF_1}{2d_1L}.$$

Since each subpopulation N_1, N_2, N_3, . . . N_n may be estimated in a similar manner, the sum of such terms will estimate N_T, the total population.

$$N_T = \frac{cF_1}{2d_1L} + \frac{cF_2}{2d_2L} + \frac{cF_3}{2d_3L} + \cdots + \frac{cF_n}{2d_nL},$$

or,

$$N_T = \frac{c}{2L}\left(\frac{F_1}{d_1} + \frac{F_2}{d_2} + \frac{F_3}{d_3} + \cdots + \frac{F_n}{d_n}\right) \qquad (2).$$

This is the computation formula (2) given in the body of the paper.

Formula 2 may be viewed as an expression involving the denominator of the harmonic mean of observed flushing distances, when such a mean is stated as:

$$\frac{F_1 + F_2 + F_3 + \cdots + F_n}{\frac{F_1}{d_1} + \frac{F_2}{d_2} + \frac{F_3}{d_3} + \cdots + \frac{F_n}{d_n}}.$$

Substituting the value of F_1 as stated in formula 4, and the similar values of F_2, F_3, . . . , F_n, the harmonic mean becomes:

$$\frac{\frac{2d_1LN_1}{c} + \frac{2d_2LN_2}{c} + \frac{2d_3LN_3}{c} + \cdots + \frac{2d_nLN_n}{c}}{\frac{2d_1LN_1}{cd_1} + \frac{2d_2LN_2}{cd_2} + \frac{2d_3LN_3}{cd_3} + \cdots + \frac{2d_nLN_n}{cd_n}},$$

or,

$$\frac{N_1d_1 + N_2d_2 + N_3d_3 + \cdots + N_nd_n}{N_1 + N_2 + N_3 + \cdots + N_n}$$

which is the arithmetic mean of all flushing distances throughout the entire population (formula 3). Thus the harmonic mean of observed flushing distances estimates the arithmetic mean of all flushing distances, and might be used in making an estimate of the population. Unless the average flushing distance of all animals is desired of itself, formula 2, which reaches an identical population estimate with less labor, might better be used.

Regarding the matter of the expected average of angles of observation in the absence of the type of error described by Webb (1942), a rough approximation may be computed from Figure 1. If the strip extending to either side of the observer's path for a distance equal to the flushing distance is divided into a number of narrow strips of equal width (consequently equal area and equal population), then an equal number of animals will be flushed from each narrow strip. The sine of each angle of observation will equal the perpendicular distance from the animal to the observer's line of travel divided by the flushing distance. In Figure 1, considering one side only, if there were a single animal flushed at the center of each strip, the 10 angles observed, and their average value, would be as follows:

Sine	Angle	Sine	Angle	
0.05	2° 52′	0.55	33° 22′	Sum—
0.15	8° 38′	0.65	40° 32′	325° 43′
0.25	14° 29′	0.75	48° 35′	Average—
0.35	20° 29′	0.85	58° 13′	32° 34′ 18″
0.45	26° 45′	0.95	71° 48′	

Since the distribution of angles of observation is the same for all values of the flushing distance, the average of all angles of observation should be approximately the same, no matter what the combination of flushing distances observed. The average value by this crude method changes as more parallel strips are assumed.

Professor Leo Katz, of the Mathematics Department, Michigan State College, has been kind enough to furnish the following general solution of this problem, used here with his permission:

$$x = \sin \theta$$

Assuming x may take any value between 0 and 1 with equal probability gives for the probability distribution of x,

$$dF(x) = 1 \cdot dx, \qquad 0 \leqq x \leqq 1$$

and for the probability distribution of θ,

$$dF(\theta) = 1 \cdot \cos \theta d\theta, \quad 0 \leqq \theta \leqq \frac{\pi}{2} \text{radians.}$$

The mean value of θ is, then,

$$\bar{\theta} = \int_0^{\pi/2} \theta \cos \theta d\theta = \frac{\pi}{2} - 1 \text{ radians,}$$

or,

$$\bar{\theta} = 32^\circ\ 42'\ 15.2'' \text{ radians.}$$

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GROWTH OF NORRIS RESERVOIR WALLEYE DURING THE FIRST TWELVE YEARS OF IMPOUNDMENT[1]

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Limited information on growth of walleye (*Stizostedion v. vitreum*) in Norris Reservoir (Tennessee) during the first five years of impoundment has already been discussed (Eschmeyer and Jones, 1941). Additional data for this period and for the next seven years of impoundment are now available. These data, together with information on growth trends for the twelve years

[1] Published by permission of the Tennessee Valley Authority. Mr. D. E. Manges assisted by calculating "K" values for 750 fish.

(1936–1947) are presented below. Similar growth studies for four other Norris Reservoir species—smallmouth bass (*Micropterus dolomieu*), spotted bass (*M. punctulatus*), largemouth bass (*M. salmoides*), and black crappie (*Pomoxis nigro-maculatus*)—have been published (Stroud, 1948);[2] one for sauger (*Stizostedion canadense*) is in progress.

Spawning of bass and black crappie has apparently been successful each year of impoundment, due partly to the fact that surface elevation normally rises slowly or remains steady during the spawning period. Spawning of walleye in Norris Reservoir or its tributaries (so far unobserved) has apparently been successful each year also. Some evidence, however, suggests that certain conditions were more favorable to survival of walleye in some years than in others.

It is already known that growth rates of Norris basses and crappie increased significantly during the seventh year of impoundment (1942) and that average growth rates for the second five years of impoundment equalled those for the first five years. There was an apparent correlation, common to all these species, between the long-term cycle of spring and early summer water levels and certain pronounced annual fluctuations in growth-rates It was concluded that significant increases in growth-rates in 1942 were due to the flooding of extensive areas of shore zone which had become verdant during previous years of low maximum water levels.

Walleye, too, continue to grow rapidly in Norris Reservoir despite the pronounced increases in population density that have undoubtedly occurred in recent years. Preliminary inquiry suggests that this may also be true in part for sauger.

[2] All references to Norris Reservoir basses and black crappie, unless otherwise noted, refer to this publication.

GENERAL INFORMATION

This study is based on the analysis of scale samples from 1,210 walleye taken in Norris Reservoir. Most of them (940 fish) were taken in gill nets of various mesh size by hook and line (187 fish), and with derris (68 fish). A few (15 fish) were captured in sinkholes, caught with seines or picked up while floating at the surface of the water in a weakened condition. The numbers of fish collected by calendar years were as follows: 1942—36, 1943—321, 1944—252, 1945—63, 1946—276, 1947—213, 1948—49. Fish representing the hook-and-line catch were collected principally in 1942, 1946, and 1947. Most of those taken with derris were collected in 1947.

Details of the methods used in studying age and growth of game and pan fish in TVA impoundments have already been discussed (Stroud, *op. cit.*).

The generally accepted scale method was assumed to be valid for this study. Individual growth histories were calculated by direct proportion, partly for ready comparison with previously published data. Schloemer and Lorch (1942) also based their calculations on the assumption that scale length and body length increased in direct proportion to each other. Carlander (1945), on the other hand, showed this to be inaccurate for Lake of the Woods wall-

eye. If the relationship determined for the latter fish were applied to Norris walleye, first-year calculated lengths would be about 10 per cent greater and second-year lengths would be about 4 per cent less. Comparison of average calculated first-year lengths with average measured first-year lengths, however, suggests that determinations of individual growth histories by direct proportion are highly accurate for Norris walleye.

Only two scale samples, both from large males, could not be read. Age determinations were easily made for all other fish and are believed to be correct.

Fish included in any age group, designated by arabic numerals, do not necessarily have the same number of annuli on their scales. Fish in age group 3, for example, would have 2 annuli plus a full year's postannular growth on their scales if caught between December 1 and the time of annulus formation the following spring. Scales of other fish included in age group 3 would have 3 annuli plus some post-annular growth if caught between the time of annulus formation in spring and November 30 of the same year.

All averages are weighted arithmetic means. Lengths expressed in millimeters refer to standard length; those expressed in inches refer to total length. Minimum legal length is 15 inches. Growth of Norris walleye is compared with growth in other scattered waters for which published data are readily available to the writer. Some mimeographed material, presumably in preliminary form, is referred to in the text but not listed with published data. Comparative figures published only as standard lengths were converted to total length by using appropriate conversion factors supplied by the author cited or determined from Norris fish (Table 1).

TABLE 1.—THE RELATIONSHIP OF TOTAL LENGTH TO STANDARD LENGTH IN MILLIMETERS EXPRESSED AS THE RATIO T.L./S.L., BY 20 MILLIMETER STANDARD LENGTH SIZE GROUPS. FACTORS FOR CONVERTING STANDARD LENGTH IN MILLIMETERS TO TOTAL LENGTH IN INCHES INCLUDED

Standard Length by 20 Millimeter Groups	Number of Fish	T.L./S.L.	Conversion Factor
100–119	1	1.248	0.0491
120–139	11	1.214	0.0478
140–159	23	1.210	0.0476
160–179	14	1.206	0.0475
180–199	7	1.208	0.0476
200–219	10	1.203	0.0474
220–239	4	1.207	0.0476
240–259	8	1.203	0.0474
260–279	18	1.189	0.0468
280–299	36	1.193	0.0470
300–319	64	1.191	0.0469
320–339	98	1.189	0.0468
340–359	86	1.187	0.0467
360–379	147	1.184	0.0466
380–399	208	1.181	0.0465
400–419	182	1.180	0.0465
420–439	121	1.177	0.0463
440–459	64	1.175	0.0463
460–479	21	1.176	0.0463
480–499	19	1.171	0.0461
500–519	5	1.177	0.0463
520–539	9	1.171	0.0461
540–559	4	1.176	0.0463
580–599	2	1.168	0.0460
600–619	3	1.168	0.0460
640–659	3	1.163	0.0458
660–679	1	1.162	0.0457
Total or average	1,169	1.184	0.0466

The distribution of walleye used in the study is shown by length and method of capture in Table 2. While each size mesh of gill net (expressed as bar measure) tended to select a certain average size of walleye, there was much overlapping in size of fish caught by the two important meshes ($1\frac{1}{2}$″ and 2″). Other size meshes (1″,

2½", and 3") which were fished extensively captured few walleye. The gill nets were fished from March to November in 1943 and 1944 with from 10 to 73 fish being taken each month. In later years gill nets were fished from December to March. Scale samples representing hook-and-line catches were collected largely in May and June, 1946 and 1947. While scale samples from fish taken by hook and line numbered only one-fifth as many as those from walleye taken in gill nets, the length range of fish taken by each method was similar. Derris samples were secured in fall and early winter. The paucity of fish in the distribution between 220 and 260 millimeters reflects rapid spring growth by one-year-olds.

TABLE 2.—STANDARD LENGTH FREQUENCY DISTRIBUTION OF 1,210 NORRIS RESERVOIR WALLEYE BY METHOD OF CAPTURE, 1942–1948 CAPTURES

Standard Length by 20 Millimeter Groups	Method of Capture							Total all Methods
	Gill net (bar measure)				Total gill net	Hook and line	Derris samples[2]	
	1"	1½"	2"	X[1]				
100–119							1	1
120–139							11 (2)	11
140–159							23 (4)	23
160–179							15 (1)	15
180–199	4				4	1	2	7
200–219	2				2		10 (2)	12
220–239	2				2		2 (1)	4
240–259		1			1	1	6	8
260–279		16	1		17	1	2	20
280–299	1	28	2		31	3	2	36
300–319		51	5	3	59	4	3	66
320–339		79	8	3	90	12		102
340–359		36	16	18	70	16	1	87
360–379		12	51	38	101	50		151
380–399		13	121	38	172	45		217
400–419		11	136	22	169	16	(1)	186
420–439		3	79	27	109	15		124
440–459		4	40	17	61	7		68
460–479		1	12	4	17	5		22
480–499		1	11	3	15	5	(1)	21
500–519			2	3	5	1		6
520–539			2	3	5	4		9
540–559			1	2	3		1	4
580–599			1		1	2[3]		3
600–619			2	1	3			3
640–659			1	1	2	1		3
660–679			1		1			1
Total	9	256	492	183	940	189	81 (12)	1,210

[1] Size mesh not designated. It is known, however, that most of these fish were taken in 2" mesh although a few were taken in the 1½" mesh; 2 fish 480–499 mm., 2 fish 540–559 mm., and 1 fish 640–659 mm. were taken in 2½" mesh; 1 fish 520–539 mm. was taken in 3" mesh.

[2] Includes a few fish taken with a minnow seine, numbers indicated in parentheses, and 1 fish 240–259 mm. taken in a sinkhole.

[3] Includes one fish 26¼" long; standard length estimated to fall in this group.

A wide range in growth potential was undoubtedly sampled by the gill nets as about two-thirds of all fish taken in them were caught in successive months

throughout most of the growing season. This is supported further by comparing growth rates calculated separately for fish taken by the two most important methods. For example, 27 two-year-old males taken in gill nets during December 1945 ranged from 318 to 395 millimeters in length and averaged 365 mm. Similarly, 25 two-year-old males taken the following spring by hook and line had lengths before renewal of growth ranging from 312 to 384 mm. and averaging 362 mm. In another instance the difference between means, although somewhat greater, was still not significant. Here 31 female two-year-olds taken in gill nets in December 1945 ranged from 282 to 400 mm. and averaged 369 mm. Sixteen female two-year-olds taken by hook and line in the spring of 1946 varied from 304 to 383 mm. and averaged 354 millimeters. This would seemingly indicate that little error results from combining data for all fish irrespective of method of capture.

TABLE 3.—STANDARD LENGTH-FREQUENCY DISTRIBUTION OF 1,202 NORRIS RESERVOIR WALLEYE BY AGE, 1942–1948 CAPTURES

Standard Length by 20 Millimeter Groups	Age-Group									Total
	0	1	2	3	4	5	6	7	8	
100–119	1									1
120–139	11									11
140–159	22	1								23
160–179	14	1								15
180–199	5	2								7
200–219	2	10								12
220–239	2	2								4
240–259	1	7								8
260–279		19	1							20
280–299		31	5							36
300–319		43	23							66
320–339		39	61	1	1					102
340–359		18	60	6						84
360–379		12	117	19	3					151
380–399		5	152	40	12	5	1	1		216
400–419			100	37	24	15	7	2		185
420–439			20	51	30	9	12	1		123
440–459			5	24	17	12	3	6		67
460–479			1	6	7	3	4		1	22
480–499			1	5	9	3	1	1	1	20
500–519				1	3	2				6
520–539					3	5	1			9
540–559						3	1			4
580–599						3[1]				3
600–619						1		1		2
640–659						1	1		1	3
660–679								1		1
Total	58	190	546	190	109	62	31	13	3	1,202

[1]Includes one fish 26¾ inches long; estimated standard length falls here.

AGE AND RATE OF GROWTH; TWELVE-YEAR HISTORY

Distribution of the fish by length and age is shown in Table 3. The overlap within successive age groups results

TABLE 4.—AVERAGE CALCULATED STANDARD LENGTH IN MILLIMETERS ATTAINED BY 1,146 NORRIS RESERVOIR WALLEYE OF VARIOUS AGE-GROUPS AT THE END OF EACH YEAR OF LIFE, 1942–1948 CAPTURES AND SEXES COMBINED

Year-Class	Year of Capture	Age-Group	Number of Fish	Calculated Standard Length (mm.) at End of Year							
				1	2	3	4	5	6	7	8
1937	1944	7	1	114	295	375	403	417	428	439	
	1943	6	12	157	312	378	412	435	454		
	1942	5	1	140	301	375	406	415			
1938	1946	8	1	138	295	375	415	437	461	472	478
	1945	7	1	149	323	395	416	426	434	441	
	1944	6	3	144	304	374	407	427	439		
	1943	5	11	164	306	381	414	429			
	1942	4	3	181	334	393	417				
1939	1947	8	1	192	328	374	403	444	464	473	483
	1946	7	3	164	303	364	395	414	428	435	
	1944	5	4	192	349	395	415	431			
	1943	4	28	214	348	402	430				
	1942	3	14	236	374	409					
1940	1948	8	1	188	340	487	560	619	630	646	655
	1947	7	5	134	270	349	395	435	451	456	
	1946	6	11	170	314	389	421	444	453		
	1945	5	1	215	371	412	422	430			
	1944	4	19	185	339	398	430				
	1943	3	59	210	359	406					
	1942	2	11	225	364						
1941	1948	7	3	165	334	415	464	500	520	532	
	1947	6	6	179	322	364	396	410	421		
	1946	5	22	196	340	408	444	459			
	1945	4	1	223	331	381	399				
	1944	3	29	191	338	407					
	1943	2	69	218	372						
	1942	1	1	272							
1942	1948	6	1	150	308	358	371	398	407		
	1947	5	16	215	361	438	473	493			
	1946	4	28	191	342	406	435				
	1945	3	1	229	389	452					
	1944	2	168	228	361						
	1943	1	139	247							
1943	1948	5	5	193	318	380	417	433			
	1947	4	14	220	378	424	445				
	1946	3	24	212	362	415					
	1945	2	2	205	380						
	1944	1	18	226							
1944	1948	4	16	202	343	388	412				
	1947	3	40	214	356	402					
	1946	2	173	226	366						
1945	1948	3	20	200	332	385					
	1947	2	97	206	338						
	1946	1	19	170							
1946	1948	2	27	200	324						
	1947	1	5	210							
1947	1947	1[1]	12	207							
Average calculated standard length				217	352	402	430	449	453	478	539
Average total length				10.3	16.4	18.7	19.9	20.8	21.0	22.1	24.9
Average annual increment				217	135	50	28	19	4	25	61
Average increment of total length				10.3	6.1	2.3	1.2	0.9	0.2	1.1	2.8
Number of fish				1,146	952	405	218	109	49	16	3

[1] These fish although captured as young-of-the-year and lacking annuli on their scales had probably completed growth for the year when captured (November 7).

partly from the fact that fish were taken throughout the growing season rather than at one particular time of the year. It reflects also the conclusion of Eddy and Carlander (1939) that there is tremendous variation in growth of walleye. In the case of Norris walleye much of this variation is due to sexual differences.

Two of the four largest fish (females) included in the sample were 30 inches long, and two were 29½ inches. Larger walleye, however, are known to occur in Norris Reservoir. Several of these have won prizes and honorable mentions in recent national fishing contests. It is probable that some extremely large specimens are one or two years older than the largest fish (7- and 8-year-olds) in the sample; however, relatively few exceed eight years of age. There probably is no walleye now living in Norris Reservoir that is as old as the impoundment.

Norris walleye average about 10.3 inches at the end of the first year of life and 16.4, 18.7, 19.9, 20.8, 21.0, 22.1, and 24.9 inches at the ends of the next seven successive years of life, respectively (Table 4). Minimum legal length is reached by most fish in late summer during their second growing season as one-year-olds. In a sample of 115 walleye caught by sportsmen during the last week of May and the first week of June, 1946, 80 per cent were two-year-olds, 12 per cent were three- and four-year-olds, 8 per cent were five- and six-year-olds. In another similar sample of 47 fish taken in 1947, 64 per cent were two-year-olds and 26 per cent were three-year-olds. Relatively few of the larger walleye in the reservoir are harvested by sportsmen although they can be sampled readily by means of gill nets.

Much older walleye have been reported from other waters, all in the north. Fourteen- and fifteen-year-old fish were recorded in Canada (Hart, 1928). Fourteen-year-olds were taken from Lake of the Woods (Carlander, *op. cit.*). In other Minnesota waters twelve- and fourteen-year-olds were found (Eddy and Carlander, *op. cit.*). On the other hand some large walleye taken (introduced species) in Candlewood Lake, Connecticut, were apparently much younger. The largest reported caught there, 28 inches long and weighing 8 pounds, was a 7-year-old (Webster, 1942).

Average lengths by year-classes and age-groups covering the first twelve years of impoundment, including previously published data for 99 fish (Eschmeyer and Jones, *op. cit.*), are presented in Table 5. These are shown graphically in Figure 1, together with trends in the form of three-year moving averages. Although growth-rates were expected to decline as the impoundment became older (Eschmeyer and Jones, *op. cit.*), age of impoundment appears to have had little influence on rate of growth so far. Growth rates actually increased gradually through 1942 among young-of-the-year and through 1943 and 1944 among successively older fish. Growth rates began to decline somewhat in the eighth to tenth years of impoundment. Even now, although the trend is slightly downward, average growth rates are as good or better than they were during the first five years of impoundment. Factors other than age of impoundment caused these recent declines in growth rate of walleye.

TABLE 5.—TWELVE YEARS' (1936–1947) GROWTH HISTORY OF 1,245 WALLEYE IN NORRIS RESERVOIR, EXPRESSED AS AVERAGE CALCULATED LENGTHS ATTAINED BY FISH OF EACH YEAR-CLASS AT THE END OF EACH YEAR OF LIFE, COMBINING DATA FOR ALL AGE-GROUPS AND BOTH SEXES; 1,146 FISH OF THE PRESENT STUDY COMBINED WITH PREVIOUSLY PUBLISHED DATA[1]

Year-class	Average calculated lengths[2] at end of year																							
	1			2			3			4			5			6			7			8		
	S	T	No.	S	T	No.	S	T	No.	S	T	No.	S	T	No.	S	T	No.	S	T	No.	S	T	No.
1936	174	7.9	24	345	15.8	24	460	21.1	24	489	22.6	10												
1937	177	8.4	75	333	15.6	75	419	19.5	75	442	20.5	25	432	20.0	14	452	20.9	13	439	20.3	1			
1938	161	7.6	19	311	14.6	19	382	17.8	19	413	18.4	19	429	19.9	16	442	20.5	5	456	21.1	2	478	22.2	1
1939	215	10.2	50	352	16.4	50	401	18.6	50	425	19.7	36	426	19.7	8	437	20.2	4	445	20.6	4	483	22.3	1
1940	202	9.6	121	347	16.2	107	400	18.6	96	426	19.7	37	450	20.8	18	463	21.4	17	488	22.5	6	655	30.1	1
1941	206	9.8	131	355	16.6	130	403	18.7	61	435	20.2	32	454	21.0	31	465	21.6	9	532	24.6	3			
1942	232	11.0	353	359	16.8	214	417	19.4	46	447	20.7	45	487	22.5	17	407	18.9	1						
1943	216	10.2	63	363	16.9	45	414	19.3	43	438	20.3	19	417	19.4	5									
1944	222	10.6	229	363	16.9	229	400	18.6	56	412	19.2	16												
1945	200	9.5	136	337	15.8	117	385	17.9	20															
1946	202	9.6	32	324	15.2	27																		
1947	207	9.8	12																					
Grand average calculated length	213	10.1		352	16.4		408	19.0		435	20.2		449	20.8		453	21.0		478	22.1		539	24.9	
Average annual increment of length	213	10.1		139	6.3		56	2.6		27	1.2		14	0.6		4	0.2		25	1.1		61	2.8	
Number of fish	1,245			1,037			490			239			109			49			16			3		

[1] Previously published data (Eschmeyer and Jones, 1941) consist of the following: 1936 year-class, 24 fish; 1937 year-class 61 fish; 1940 year-class, 14 fish.
[2] S = standard length, T = total length, and No. = number of fish used in calculation.

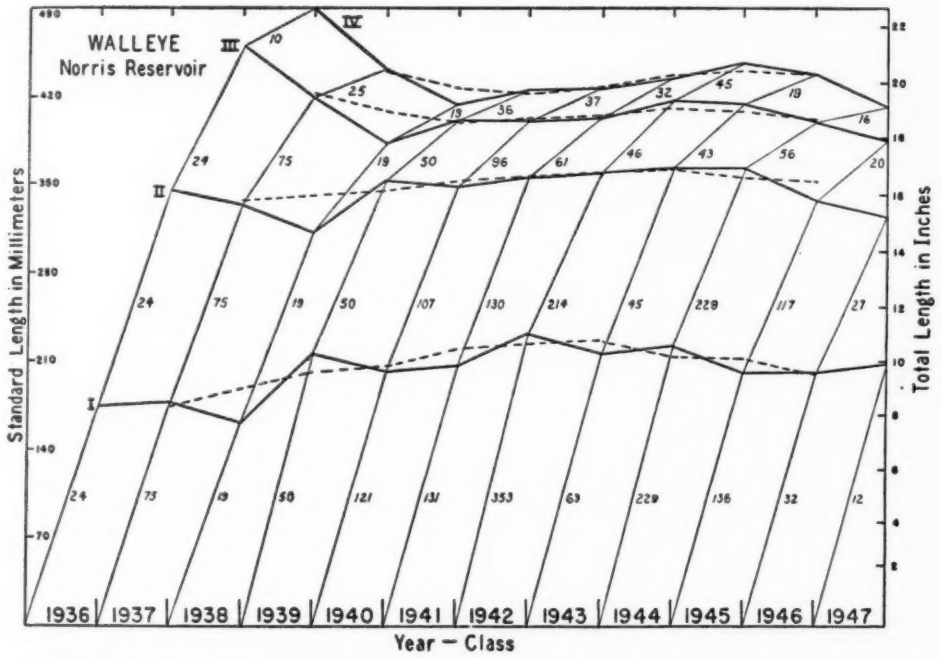

FIG. 1.—Twelve-year (1936–1947) growth history of 1,245 Norris Reservoir walleye showing growth curves by successive year-classes (light lines). Heavy solid lines connect points representing corresponding average lengths attained at ages indicated by Roman numerals. Broken lines are trend lines derived from three-year moving averages of these data. Arabic numerals indicate numbers of fish used in respective calculations.

DIFFERENTIAL GROWTH OF THE SEXES

As mentioned above a considerable difference in rate of growth between males and females occurs among Norris walleye. The oldest male was eight years old; the largest among 528 known males was 23.2 inches. Few males actually approached this length although 33 six-, seven-, and eight-year-old males were caught. Twenty-five of the 514 known females in the sample were larger than the largest male. The oldest female was eight years old but there were only 12 six-, seven-, and eight-year-old females in the sample. Actual average lengths for fish of each sex at successive ages are tabulated in Table 6 and illustrated in Figure 2. These data show that females grow more rapidly even as young-of-the-

TABLE 6.—AVERAGE TOTAL LENGTHS OF NORRIS RESERVOIR MALE AND FEMALE WALLEYE AT SUCCESSIVE AGES. NUMBERS OF FISH IN PARENTHESES

Sex	Calculated Total Length at Age							
	1	2	3	4	5	6	7	8
Males	9.8 (529)	16.0 (481)	18.1 (249)	19.1 (139)	19.6 (74)	19.9 (35)	20.4 (13)	22.2 (2)
Females[1]	10.7 (508)	17.0 (416)	19.6 (136)	21.7 (67)	23.7 (32)	24.0 (12)	29.3 (3)	30.1 (1)

[1] Since completion of the study another large female was taken in a seine 3/26/48; this fish, 31.7 inches long, was 7 years old.

year. At one year of age females averaged 0.9 inches longer and at the end of the sixth year they averaged 4.1 inches longer than males. During the seventh and eighth years females may average as much as 8.9 inches longer than males. In terms of weight, differences between

too, that large walleye might eat adult shad to some extent. More recent findings lead to the same conclusion, that most walleye feed heavily on young shad ranging in size up to 3 inches. Twenty-five walleye included in the present study had eaten shad 4 to 5

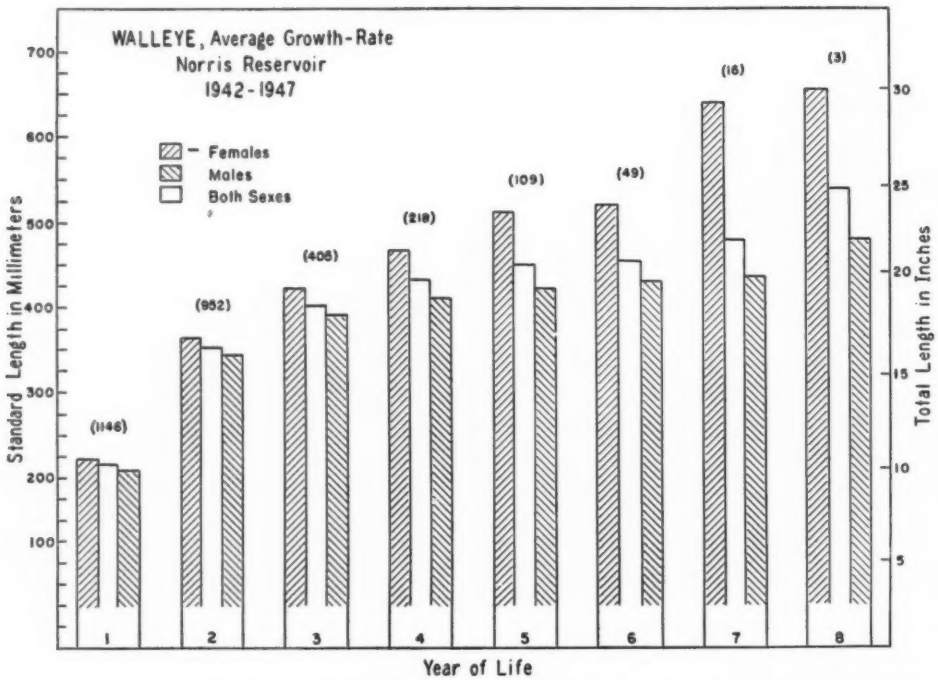

FIG. 2.—Average total lengths attained at successive ages by male and female walleye and by both sexes combined, in Norris Reservoir; 1942–1947 captures. Numbers of fish included in each age group shown in parentheses.

males and females are even more striking. Only one male in the sample went over 4 pounds and it weighed only 4.2 pounds (1919 grams); the four largest females weighed 7.8, 10.6, 11.5, and 11.9 pounds. Larger known specimens were undoubtedly females.

Dendy (1946) reported that young gizzard shad (*Dorosoma cepedianum*) constitute the principal item in the diet of Norris game fish. He suggested,

inches long (also young-of-the-year). These more recent data also confirm the suggestion that some adult shad are eaten, although it is doubtful whether walleye under 20 inches can utilize them. The three smallest walleye known to have had adult shad in their stomachs (small adult shad, one each, 8 inches long) were 20.0, 20.3, and 20.5 inches in length. It may well be significant that only one was a male.

TABLE 7.—GROWTH OF WALLEYE IN NORRIS RESERVOIR AND IN OTHER WATERS. APPROXIMATE TOTAL LENGTHS IN INCHES. NUMBERS OF FISH NOT INCLUDED (SEE ORIGINAL SOURCE). FIGURES IN PARENTHESES ARE ORIGINAL FIGURES WHERE TOTAL LENGTHS WERE NOT GIVEN, CORRESPONDING TOTAL LENGTHS BEING ESTIMATED AS IN FOOTNOTES

Water and Source	Average Lengths Attained at End of Year														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Norris Reservoir	10.3	16.4	18.7	19.9	20.8	21.0	22.1	24.9							
Lake Abitibi (Hart, 1928)[1]		8.0 (175)		11.5 (252)	11.8 (260)	12.8 (280)	13.9 (306)	17.6 (386)	17.8 (390)	18.7 (401)	17.4 (382)		23.2 (508)	21.4 (470)	
Lake Nipigon (Hart, 1928)	5.6 (123)	7.7 (169)	9.4 (207)	12.5 (275)	14.2 (312)	14.4 (315)	15.3 (335)	18.5 (407)	19.4 (426)	20.8 (457)	21.5 (472)	22.5 (492)		24.4 (535)	26.1 (572)
Lake Winnipeg (Bajkov, 1930)[2]	7.3 (160)	10.5 (230)	13.2 (290)	15.0 (330)	16.4 (360)	17.8 (390)	18.9 (415)	19.6 (430)	19.8 (435)	20.2 (443)					
Lake of the Woods (Carlander, 1945)[1]	6.4 (141)	9.3 (203)	11.5 (253)	13.4 (295)	14.8 (326)	16.7 (366)	18.2 (400)	19.9 (437)	21.6 (474)	22.7 (498)	23.9 (524)	24.3 (532)	25.6 (561)	26.4 (580)	
81 Minnesota Lakes and Streams (Eddy and Carlander, 1939)	4.6	8.6	12.0	15.0	18.1	20.5	22.9	25.2	26.7						
Bass Lake (Schloemer and Lorch, 1942)[3]	8.4 (175)	13.5 (288)	17.1 (366)	19.6 (420)	21.5 (460)	24.5 (523)									
Trout Lake (Schloemer and Lorch, 1942)	5.3	9.7	13.7	16.6	19.0	20.7	21.7	22.3	23.1	23.3					
Lake Erie (Adamstone, 1922)[4]	4.1 (103)	7.1 (180)	9.6 (244)	11.7 (297)	13.5 (344)	15.2 (387)	16.8 (427)	18.3 (465)	19.8 (502)	21.1 (535)	22.4 (569)	23.8 (602)	24.6 (625)		
Lake Erie (Deason, 1933)[1]	4.1 (91)	8.3 (183)	11.3 (248)	14.9 (327)	18.0 (396)	20.9 (458)									

[1] Standard length given by authors in parentheses; total length estimated as 1.159 ×standard length (cf. Carlander 1945).
[2] Original figures in millimeters assumed to be standard length; total length estimated as 1.159 ×standard length.
[3] Standard length given by authors; total length estimated as 1.184 ×standard length.
[4] Original figures reported as total length in centimeters; figures in parentheses are total lengths in millimeters.

The stomachs of seven other walleye, all females ranging from 23.2 to 30.2 inches, contained one or more adult shad 9.0 to 13.2 inches long. These seven fish were from four to eight years old and weighed from 4.5 to 11.9 pounds.[3] The minimum size Norris walleye physically able to utilize adult shad for food appears to be about the maximum length so far achieved by the oldest known males. Many females, on the other hand, reach this same size at relatively early ages.

[3] Since completion of the study another large walleye was taken 3/26/48 in a seine. This fish, a spent female, was 31.7 inches long, 11.0 pounds in weight and 7 years old. It had a 13.0 inch shad in its stomach.

An ability to utilize adult shad for food should result in greater feeding efficiency and in more rapid growth. This undoubtedly contributed to the wide differences noted in rate of growth between sexes during later years of life. It is also coupled with the natural tendency of females to grow more rapidly. Cooper and Fuller (1945) noted somewhat similar circumstances with respect to lake trout in Moosehead Lake, Maine. They concluded that record size trout probably resulted when faster growing individuals reached a large enough size, sufficiently early in life, to ingest adult suckers that abound in that lake. It is quite possible that prize winning walleye in Norris

Reservoir are those fast-growing females that begin feeding on adult shad at an early age.

GROWTH IN OTHER WATERS

Comparing growth of walleye in Norris Reservoir with growth in other waters (Table 7) suggests that Norris growth-rates are very rapid. Figure 3 shows clearly that only walleye in Bass Lake, Wisconsin, approach Norris walleye in rapidity of growth. The Bass Lake walleye were somewhat longer as 5- and 6-year-olds, and apparently represent the fastest growing walleye population in Wisconsin. Data for Trout Lake are about the same as the Wisconsin average (Schloemer and Lorch, *op. cit.*). Average lengths of walleye from the lakes of Quetico Provincial Park, Ontario (Lindeborg, 1941) while not included in the table, were somewhat greater than those cited for Lake Winnipeg. Also not included in the comparison were some data available only in mimeographed form suggesting that Southern Wisconsin walleye grow more rapidly on the average than those inhabiting more northern Wisconsin waters (MacKenthun, 1946). In Oneida Lake, New York, 35 young-of-the-year averaged 5.25 inches on October 24, 1940, at the virtual conclusion of 1940 growth (Raney and Lachner, 1942). This is about half the length attained by young-of-the-year at the conclusion of the growing season in Norris Reservoir.

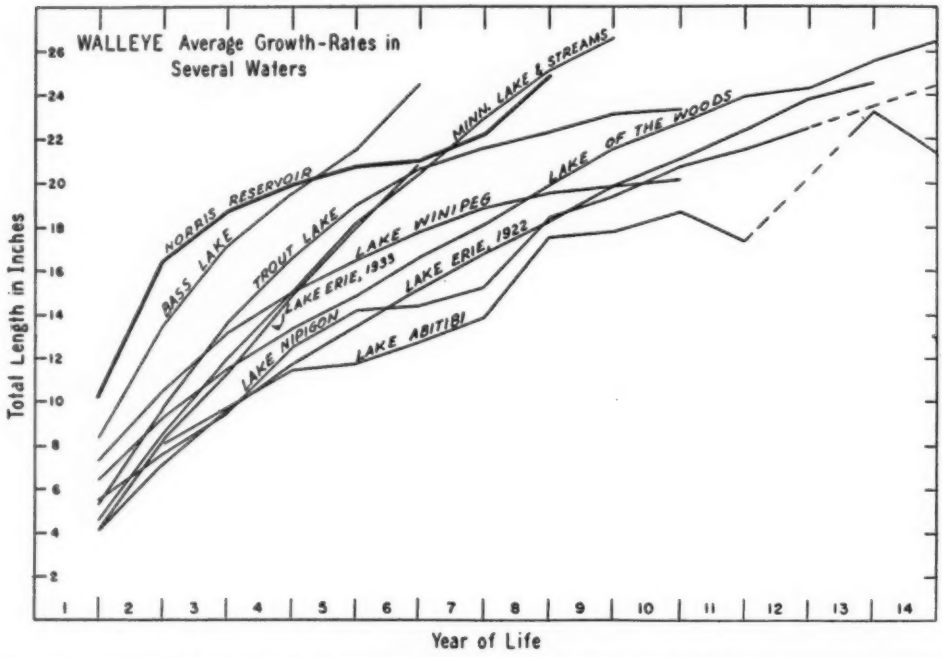

FIG. 3.—Average total lengths attained at successive ages by walleye in several waters.

In general, rapidity of growth depends largely on the amount of food

consumed, such other factors as temperature being favorable. Availability of food to individual fish is governed largely by the extent of competition. Food species in Norris Reservoir—principally gizzard shad, minnows, bluegills, black crappie, and skipjacks—are abundant. Growing seasons may be as long as 37 weeks (Stroud, *op. cit.*). Rapid growth of Norris walleye apparently results from general favorability of these two factors in the reservoir. Some evidence suggests, on the other hand, that while the yield to anglers is fairly high (Eschmeyer, Manges, and Haslbauer, 1947) population density of walleye—and the extent of competition—may be subject to cyclic fluctuation. This will be discussed in detail beyond.

INTRA-SEASONAL GROWTH

As noted above growth rates depend largely on the amount of food consumed and upon its relative availability to each fish. Heredity limits growth potential at some unknown point. Walleye might be expected to grow rapidly throughout the growing season in an environment well supplied with small fish. This is not at all the case, however, in Norris Reservoir. Table 8 and Figure 4 summarize percentages of seasonal growth attained during successive semi-monthly periods by fish of several age groups. These fish were all taken in gill nets during the growing seasons of 1943 and 1944. Percentages of seasonal growth attained during successive periods were similar for both sexes although actual increment was greater in each period among females. Data for the two years were combined only after separate tabulation revealed complete agreement. Most of the one-year-olds were caught in 1943 and most of the two-year-olds were caught in 1944. The proportions of three- and four-year-olds were similar in each year. The figures on latest fall growth

TABLE 8.—PER CENT OF YEARLY GROWTH ATTAINED DURING SUCCESSIVE SEMI-MONTHLY PERIODS BY NORRIS RESERVOIR WALLEYE OF SEVERAL AGE-GROUPS; 1943–1944 CAPTURES AND SEXES COMBINED.[1] CUMULATIVE PER CENT OF GROWTH (FIRST FIGURE) AND NUMBERS OF FISH ENTERING CALCULATIONS (SECOND FIGURE) IN PARENTHESES

Semi-monthly period	Age-group					Average 1–4
	0[2]	1	2	3	4	
April 30			*8* (*8*, 10)	*19* (*19*, 3)		*11* (*11*, 13)
May 15		*5* (*5*, 3)	*6* (*14*, 7)	*0* (*19*, 5)		*4* (*15*, 15)
May 30		*6* (*11*, 3)	*6* (*20*, 15)	*3* (*22*, 6)	*12* (*12*, 7)	*7* (*22*, 31)
June 15		*7* (*18*, 5)	*14* (*34*, 18)	*12* (*34*, 7)	*26* (*38*, 6)	*15* (*37*, 36)
June 30		*14* (*32*, 14)	*7* (*41*, 17)	*16* (*50*, 8)	*5* (*43*, 1)	*11* (*48*, 40)
July 15		*3* (*35*, 17)	*5* (*46*, 16)	*0* (*50*, 8)	*7* (*50*, 5)	*4* (*52*, 46)
July 30		*11* (*46*, 17)	*3* (*49*, 39)	*0* (*50*, 11)	*0* (*50*, 4)	*4* (*56*, 71)
August 15	(*69*, 6)	*9* (*55*, 32)	*14* (*63*, 22)	*6* (*56*, 3)	*12* (*62*, 3)	*12* (*68*, 60)
August 30	*4* (*73*, 42)	*6* (*61*, 16)	*9* (*72*, 21)		*26* (*88*, 3)	*8* (*76*, 40)
September 15		*13* (*74*, 15)	*5* (*77*, 3)	*28* (*84*, 24)[4]		*16* (*92*, 42)
September 30		*11* (*85*, 4)			*6* (*94*, 14)[5]	*7* (*99*, 18)
October 15		*0* (*85*, 10)	*5* (*82*, 29)[3]			*4* (*103*, 39)
October 30	(*100*, 12)	*0* (*85*, 5)				*0* (.., 5)
November 15		*11* (*96*, 2)				
Total	*100* (60)	*96* (143)	*82* (197)	*84* (75)	*94* (43)	*103* (456)

[1] Data for both years and both sexes combined in the absence of significant differences due to these factors.
[2] Fish of August 15 period captured in 1946, others in 1947.
[3] Average of combined data for September 30 (9 fish), October 15 (11 fish) and November 15 (9 fish), distribution of increment being similar and resulting largely from too few fish caught during fall.
[4] Average of combined data for August 30 (3 fish), September 15 (13 fish), September 30 (5 fish), and October 15 (3 fish), distributions of increment being similar and resulting largely from too few fish caught in fall.
[5] Average of combined data for September 15 (2 fish), September 30 (6 fish), and October 15 (6 fish), distribution of increment being similar and resulting largely from too few fish caught in fall.

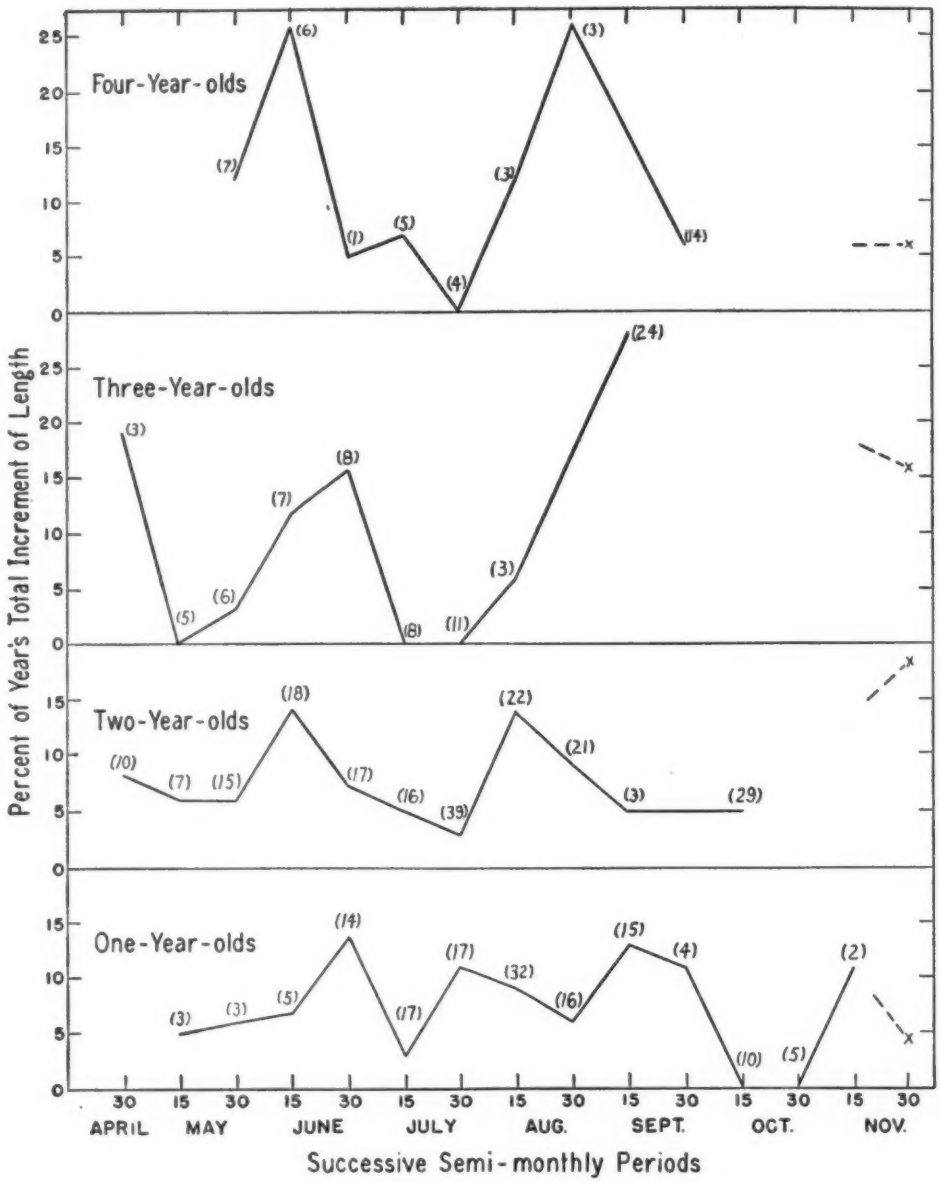

FIG. 4.—Percentages of seasonal growth attained during successive semi-monthly periods by walleye of several age groups in Norris Reservoir.

for the three oldest age groups represent averaged data for more than one fall period because fall catches were too few in number to establish the true pattern of late fall growth.

Early spring growth, when temperatures are low, is relatively slow among one-year-olds; it is more rapid among older and larger fish that are capable of eating small adults of other species. Late spring growth, following the hatch of all species, is generally rapid. During early and midsummer, on the other hand, little or no growth occurs among two-, three-, and four-year-old walleye. Growth of one-year-olds is irregular during this period but somewhat less rapid as well. Late summer growth is again rapid, and diminished growth must have occurred in fall.

This striking irregularity of intra-seasonal growth rates suggests that forage species, while abundant in Norris, may not be abundantly available at all times in the strata of water "preferred" by the walleye.[4] Walleye in Norris move to deeper and cooler strata at about the time growth rates decline so abruptly in early summer (Cady, 1945; Dendy, 1945). The vertical movements of young-of-the-year forage species are not so precisely known. It is a matter of general observation by TVA biologists, however, that the young of many species school, or are abundant, at or near the surface until early August and then suddenly disappear. Walleye, in contrast to the closely related yellow perch, apparently do not readily invade less suitable strata of water in search of food. This undoubtedly accounts in part for the experiences of local fishermen who have learned that deep-trolling in Norris during the early summer period may be more successful than at other times.

Most growth of walleye in age groups 1–4 appears to be concluded by mid-October. Limited data on growth of young-of-the-year suggest that their growth is rapid in late summer. Six young walleye caught August 13, 1946, averaged 6.6 inches and had completed about 69 per cent of the year's growth. Forty-two young taken September 3, 1947, averaged 7.2 inches and had completed 73 per cent of that year's growth. Twelve others taken November 7, 1947, averaged 9.8 inches and had completed their annual growth. The largest of the latter group was 11.6 inches long. In Oneida Lake, New York, in 1940, growth of young walleye was virtually completed by mid-September (Raney and Lachner, *op. cit.*).

Stomachs of Norris walleye taken in winter are generally well filled with gizzard shad. No growth, however, occurs in winter[5] and feeding at winter tem-

[4] During investigations of the food of Norris walleye (Dendy, *op. cit.*) irregular increases occurred in the numbers of fish taken with empty stomachs. In general, less rapid growth occurred at these same times.

[5] Seventy walleye with scales bearing one annulus were taken in gill nets at intervals between December 5, 1945, and January 11, 1946. The first group (15 fish) caught from the fifth to the seventh of December averaged 143 mm. of 1945 growth. Twenty-five caught between the eleventh and fourteenth of December had an average 1945 growth of 138 mm. Thirty more taken between January 1 and 11, 1946, had attained an average second-year increment of 148 mm. Average calculated second-year growth of 173 fish of the same year class caught during 1946 was 140 mm. During three successive netting periods of the following winter 27 fish of similar age had grown an average of 129

peratures merely provides maintenance diets for winter activities and results in a general fattening.

CONDITION AND LENGTH-WEIGHT RELATIONSHIP

An average value of condition ("K") for 57 young-of-the-year was 1.38, and for all older walleye used (1,087 fish) was 1.51. Calculations made for 1,151 fish show that weight increased approximately as the 3.1 power of increases in length up to about 26 inches and 7 pounds. This relationship may be described as follows, where W = weight in grams, and L = length in millimeters:

$$W = 0.85276 \times 10^{-5} L^{3.097},$$

and is illustrated by the curve in Figure 5 (fitted to the empirical averages of successive 10 millimeter length intervals).

Spatial limitations prevent further analysis at this time of the contributing data.

POPULATION CHANGES; YEAR-CLASS DOMINANCE

The influence of population density on growth rates of Norris Reservoir fishes is difficult to evaluate even though, as pointed out earlier for basses and crappies, it may be quite important. Norris game and pan fish are at least moderately abundant because the total annual yield to fishermen is considerable. Increased annual yields due to removal of the closed season in 1944 were accompanied by small increases in growth rates. It is obscure, however, whether this increased harvest actually caused these changes in growth rate (through temporary reduction of population density and lessened competition) because significantly lengthened growing seasons also occurred in these years.

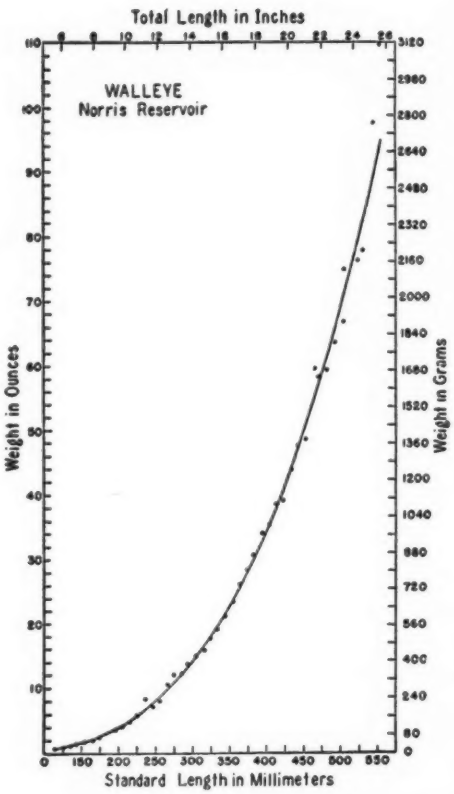

FIG. 5.—Relationship of length to weight among 1,151 walleye collected in Norris Reservoir in the period 1942–1947; sexes combined

Recent increases in the catch of walleye, sauger and basses by sportsmen have been accompanied by a decline in the catch of crappie. This decline in the

mm., 25 fish had added an average 139 mm., and 14 others had grown an average of 132 mm. in 1946. Average calculated growth for 97 fish of the same year class caught in 1947 was 132 mm. While the exact limitation of seasonal growth cannot be determined from these data it is reasonably certain that no increases in length occur after the end of November.

Norris crappie catch may have resulted partly from recent low summer water levels which created more difficult crappie fishing conditions. Bass or walleye, not both, are usually abundant from time to time in the same lake. If decreases noted in the crappie catch also reflect some declines in abundance, the simultaneous increase of bass and walleye in Norris has a possible explanation. Both walleye and bass feed heavily on crappie at times so that the abundant crappie may act as a buffer to soften or eliminate the effects of inter-specific competition usually apparent between the two (Stroud, *op. cit.*). Data reflecting changes in the population density of walleye in Norris Reservoir (Table 9) show that both the sport and experimental net catches of walleye have increased steadily since the beginning of year-round fishing in 1944. This appears to be due largely to increased numbers of walleye in the reservoir.

The spring, summer, and fall gill-net catches (standardized equipment and methods) resulted in a somewhat greater catch in 1944 than in 1943 (Table 9). A breakdown of the catch data for these years by age groups revealed decided dominance of the Norris walleye population by fish of the 1942 year class. Between March and October 1943, inclusive, 150 one-year-olds, 57 two-year-olds, 61 three-year-olds, 27 four-year-olds, plus a number of older fish, were caught. During the comparable 1944 netting operations, on the other hand, only 16 one-year-olds were taken while 159 two-year-olds were caught. The 1944 catch also included 30 three-year-olds, 17 four-year-olds, and a lesser number of older fish.

TABLE 9.—CHANGES IN THE CATCH OF NORRIS WALLEYE BY HOOK AND LINE (SPORT CATCH) AND BY GILL NETS (EXPERIMENTAL, TVA) DURING SEVERAL SUCCESSIVE YEARS

Year	Hook and Line[1]		Gill Nets[2]	
	Season[3]	Catch per 100 Fishing Trips	Season	Corrected Total Catch
1940	Summer	5		
1943			Spring, summer, and fall	196
1943	.....	..	Winter	6
1944	Summer	5	Spring, summer, and fall	229
1944	Spring	7	Winter	21
1945	Spring	11	Winter	59
1046	Spring	15	Winter	128
1947	Spring	16	Winter	139

[1] Eschmeyer, Ms.

[2] Net sets for summer periods were comparable to each other; the catch of net sets during winter were corrected to include only comparable net sets from year to year. Unusually low water levels in late January and early February 1948 interfered with netting operations and, too, some brief location changes contributed an unknown effect on total catch for the 1947–1948 winter period. Winter catches for 1946–1948 are unpublished data, others from published reports (Eschmeyer and Haslbauer, 1946; Haslbauer and Manges, 1947).

[3] Spring is from April 1 to June 30; summer is from July 1 to October 30; winter is from December 1 of year indicated to March 15 of succeeding year.

DISCUSSION

Walleye in Norris Reservoir, now in its thirteenth year of impoundment, continue to grow rapidly (as do basses

and black crappie) and are at present growing as rapidly as they did during the initial few years of impoundment. Gradually increasing trends in growth rates characterized the species during the first seven to nine years of impoundment while more recent decreases have extended through the twelfth year. The most rapid growth of young occurred in 1942, the seventh year of impoundment. A pronounced increase in survival of young also occurred that year.

As was pointed out for basses and black crappie, significant increases in growth rate that occurred in 1942 were apparently correlated with a long-term cyclic pattern of maximum spring and early summer water levels. It was also suggested that increased survival of young fish of many species probably occurred in 1942 because of increased food supplies resulting from the decay of vegetation that was flooded for the first time in several years. That this actually occurred in the case of walleye is clear from the data in the preceding section. So far as is known, Norris walleye prey on most available species but are preyed upon by none. How much strict cannibalism occurs among Norris walleye is unknown.

The increasing growth-rate trend of walleye through the seventh year of impoundment was not closely correlated with the changes occurring in the relatively shallow littoral zone as were growth rates of basses and black crappie. Walleye, however, seek deep water during most of the growing season and might not be expected to reflect these changes as clearly. Some available information suggests that this pattern of walleye growth was correlated with gradually improving food supplies over this period.

Kuhne (1939) stated, for example, that during the initial few years of impoundment minnows were the most abundant food item available to game fish at all depths. He also recorded an abundance of shad. Repeatedly since then derris sampling operations by TVA biologists have revealed that gizzard shad are extremely abundant. Minnows also are abundant and are apparently increasing in numbers annually. Measurement of many thousands of young-of-the-year shad taken with derris suggests also that their average first-year growth has declined gradually as their number has increased. Since they are plankton feeders and form large schools young shad would seem to be vulnerable to the effects of intensified competition for food.

Crappie have also increased tremendously in number (at least through the tenth year of impoundment). Since walleye feed heavily on shad and crappie in Norris Reservoir, there appears to be a simple and logical explanation for increasing rates of growth during the first seven years of impoundment—an increasing abundance of food. This period was climaxed by unusually favorable survival conditions in 1942.

Later, particularly during 1944, 1945, and 1946 (ninth, tenth, and eleventh years of impoundment), growth rates declined significantly. This undoubtedly resulted from the significant increases in population density following the extraordinary success of the 1942 spawning. (Sauger also increased in number during this period. Although their diets are similar, the extent to which sauger

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and walleye actually compete for their food is not definitely known.) The long-term cycle of spring and early summer water levels leading to significantly improved growth and survival conditions in 1942 (Stroud, *op. cit.*) undoubtedly contributed an important weight of fish to the increased catch due to removal of the closed season in 1944 (Eschmeyer and Manges, 1945).

Present food supplies are certainly adequate for present levels of population density. In addition, the long-term cycle of water-level fluctuations to date, and the long growing seasons appear to have been important factors in maintaining high levels of growth rate despite recent increases among walleye in Norris Reservoir. Increased yield to fishermen due to year-round fishing contributed an unknown effect, probably favorable, to the maintenance of rapid growth.

SUMMARY

Scale samples from 1,210 Norris Reservoir walleye were studied by the scale method. Included were fish from the 1937 through 1947 year-classes taken between 1942 and 1948 during all months of the year, largely by gill nets and hook and line. Young-of-the-year were sampled with derris and seines. Samples of the sport catch consisted largely of two- and three-year-olds with a scattering of older fish. Large walleye, although present in numbers, are not readily taken by the fishermen.

The largest and oldest male (528 known males) was 23.2 inches long, weighed 4.2 pounds, and was eight years old; there were 33 six-, seven-, and eight-year-old males in the sample. The largest and oldest female (514 known females) was 30.1 inches long, weighed 11.9 pounds and was eight years old; there were 12 six-, seven-, and eight-year-old females in the sample. Larger Norris specimens entered in past national fishing contests were undoubtedly females and may have been ten or more years old.

Females grow more rapidly than males, being about 0.9 inches (average) longer at one year of age, and 4.1 inches longer at the end of the sixth year. As older fish, females may be as much as 8.9 inches longer than males. Norris walleye apparently commence to feed to some extent on adult shad (8 inches or longer) after reaching a length of 20 to 23 inches. This is near the maximum length known to be attained by males. Females, however, attain this length relatively early in life. Only one male is known to have had an adult shad in its stomach. This may be significant, along with the natural tendency of females to grow more rapidly, in explaining the greatly accelerated growth of females during later years of life and the repeated capture of prize winning fish in Norris Reservoir.

The Norris population as a whole averages about 10.3, 16.4, 18.7, 19.9, 20.8, 21.0, 22.1, and 24.9 inches at the end of each succeeding known year of life through the eighth. Walleye up to 15 years have been reported from other more northern waters but their corresponding rates of growth have been much less rapid than for the Norris fish.

Rates of growth increased through the first seven to nine years of impoundment and were probably correlated with generally increasing food supply throughout the impounded history of the reser-

voir. Growth was somewhat less rapid more recently through the twelfth year of impoundment due to significant increases in population density during this period. Present average growth rate is fully as rapid as during the first five years of impoundment.

Intra-seasonal growth is irregular among the first four age groups, with relatively rapid growth occurring in spring and early summer (June) following the hatch of all species. Growth virtually ceases at times in midsummer (July) but becomes rapid again in late summer (mid-August to mid-September). Fall growth is slow. No length increases occur between the end of November and the time of annulus formation in spring. This irregularity of seasonal growth is probably due to the tendency of walleye to remain in deep water in July and the proclivity of young fish for shallow water until late summer. Notable success of early summer deep-trolling for walleye doubtless depends on these factors.

Average "K" for 57 young-of-the-year was 1.38 while for all other fish (1,087) it was 1.51.

The length-weight relationship for 1,151 fish up to about 26 inches and 7 pounds may be described by the equation $W = 0.85276 \times 10^{-5} L^{3.097}$, increases in weight varying approximately as the 3.1 power of increases in length.

Dominance of the Norris walleye population by fish of the 1942 year-class (seventh year of impoundment) was indicated, and significant increases in population density occurred during the ninth, tenth, and eleventh years of impoundment (1944–1946). This was probably due to the long-term cycle of spring and early summer Norris water levels which results in periodic improvement in food and survival conditions.

Current water management practices, abundant available food supplies, and long growing seasons are all important factors in maintaining rapid growth of Norris walleye despite recently increased population density. Increased fishing pressure, following the institution of year-round fishing in 1944 had an unknown, but probably beneficial effect.

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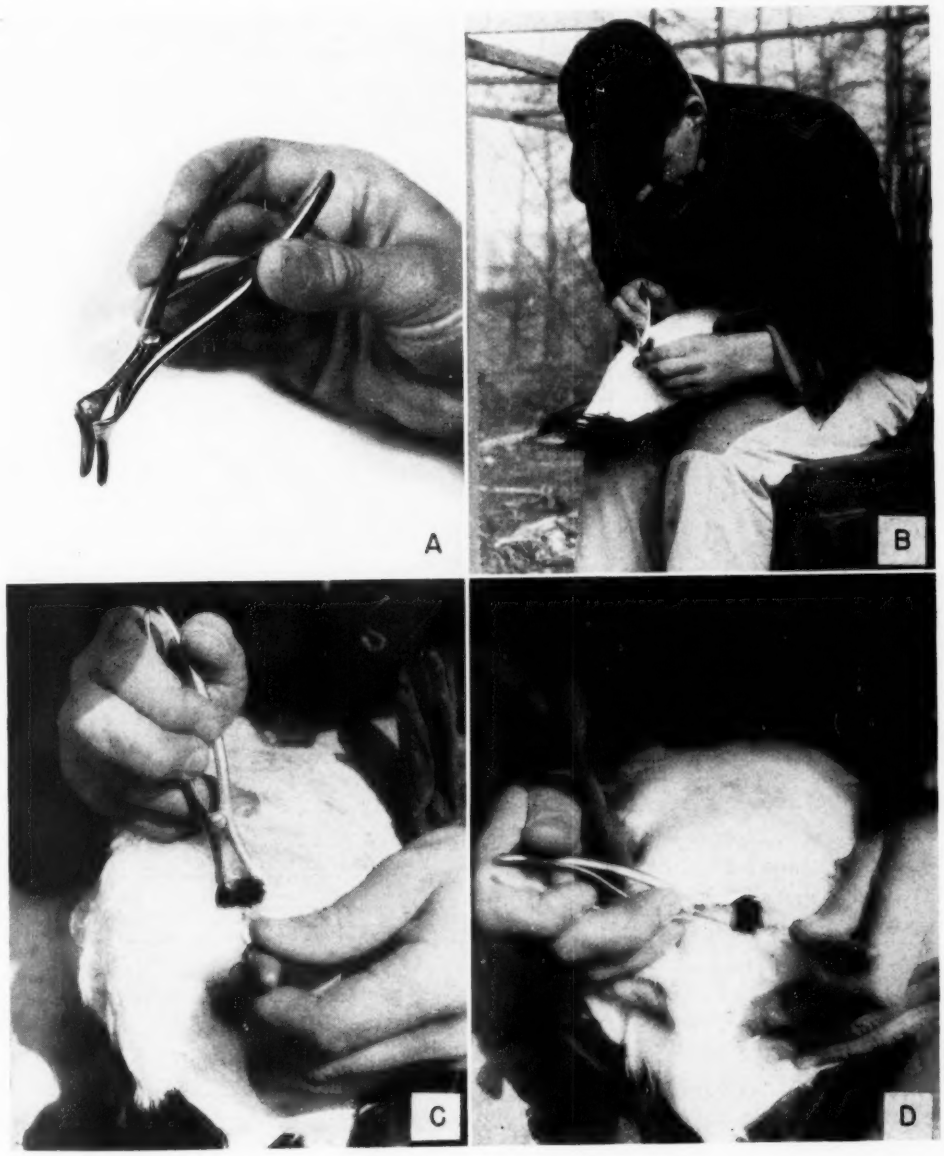

PLATE 2.—Aging Canada geese by cloacal inspection. *A*. A physician's nasal speculum. *B*. A convenient way to hold a Canada goose for cloacal inspection. *C*. Examining the bursa. *D*. Examining the oviduct.

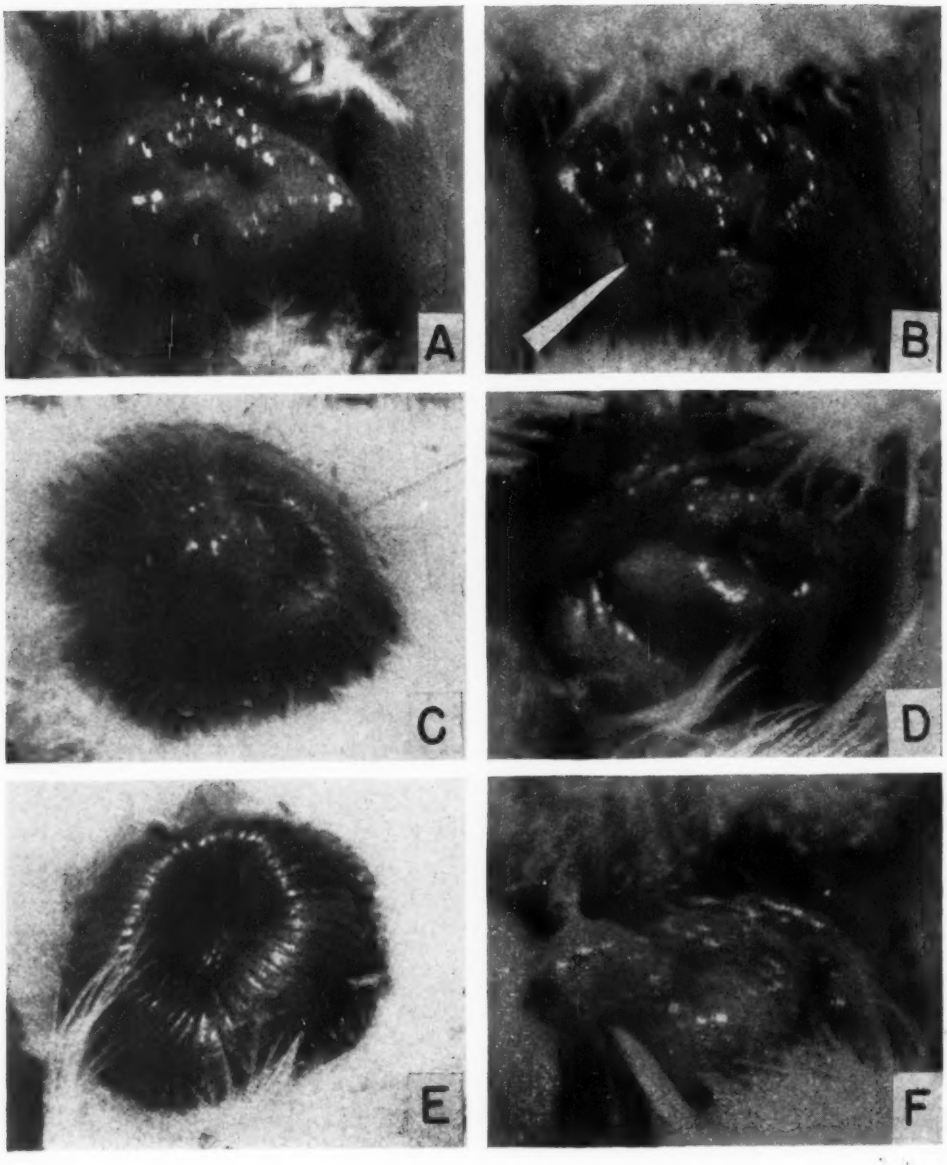

PLATE 3.—Aging Canada geese by cloacal inspection. *A*. Everted cloaca of a juvenile female. *B*. Everted cloaca of a juvenile male. Penis indicated by pointer. *C*. Naked area of the anal sphincter muscle of a yearling male. *D*. Sheathed penis of a yearling male. *E*. Naked area of an old adult male. *F*. Extended penis of an old adult male.

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METHODS OF DETERMINING AGE IN CANADA GEESE AND OTHER WATERFOWL

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The use of cloacal characters as criteria of age in waterfowl was first described by Hochbaum in 1942. In this paper he pointed out that in species of ducks that mature at the age of one year, the stage of development of the penis in the male, the presence or absence of an occluding membrane over the opening of the oviduct in the female, and the presence or absence of a bursa of Fabricius (at least as indicated by the presence or absence of an open-

[1] H. Albert Hochbaum kindly read an early draft of this paper, submitted to him in 1945, and offered a number of helpful suggestions.

ing) in both sexes, were, in the autumn, reliable bases for distinguishing juvenile from all older individuals.

The applications of these findings to Canada geese (*Branta canadensis interior* Todd.) were first studied at the Horseshoe Lake Game Refuge, Illinois, by Arthur S. Hawkins, later by William H. Elder, and from 1943 to 1946 by the writer.

To date, the condition of the oviduct and bursa has been useful chiefly in aging dead birds, as the cloaca can be rapidly and easily dissected and the bursa probed, or the presence or absence of an occluding membrane over the oviduct noted. With live birds, however, these criteria have not been fully exploited because relaxing the anal sphincter in order to examine the cloaca by the use of a local anesthesia, as recommended by Hochbaum (1942) and Elder (1946), is time consuming and is impractical in the field. To circumvent this time loss, a physician's nasal speculum, Plate 2, *A*, has been employed by the writer at Horseshoe Lake since 1944 in making cloacal examinations of Canada geese. Preliminary investigations as to its usefulness in aging ducks were made by the writer in 1947 at the Chautauqua National Wildlife Refuge near Havana, Illinois.

OPERATIONAL PROCEDURES

Handling a live Canada goose is a simple matter if it is originally grasped firmly across the humeri with one hand. Seated comfortably, the worker can then quickly turn the bird upside down and hold it securely on his lap as shown in Plate 2, *B*. Best results are obtained if the neck and head of the goose are held snugly between the legs. This latter procedure effectively reduces "nipping." Handling ducks presents less ofa problem. If a holding box is used, the individual can be held snugly between the forearms and chest with its back down on the top of the box, leaving both hands free to handle the probe and speculum.

Examination of the cloaca of waterfowl with use of a speculum is simple and, with a little practice, can be done with great rapidity. The method of examining the bursa with the aid of the speculum and probe is shown in Plate 2, *C*. With the cloaca distended, exploration for the bursa is greatly facilitated. When the left wall of the cloaca is explored for the opening of the oviduct, the axis of the speculum is held at right angles to that of the goose's body, as shown in Plate 2, *D*. Essentially the same handling techniques hold true for ducks although the entire procedure is more rapid in the case of smaller species.

An ordinary eye dropper fashioned in the manner suggested by Kirkpatrick (1944) was used as a probe. It was found that no harm was done in using a speculum if the cloaca was spread open quickly and with firm pressure at the outset. Numerous gingerly-made attempts, besides causing a bird to resist strenuously, are apt to rupture small blood vessels in the cloaca, though no permanent damage may be done when this happens. Insertion of the speculum into the cloaca is facilitated if the instrument is first dipped in a light oil.

CANADA GEESE

In discussing the technique as used with this species we are dealing primar-

ily with cloacal age characters that are of value in separating yearling geese from older adults, but for the sake of completeness, other criteria that identify juveniles are briefly mentioned. The discussion is based on data obtained in banding 3,994 geese at Horseshoe Lake between 1943 and 1946. Besides this number, 827 geese that returned to the traps in later years were handled, thus making it possible to secure information on birds of known age and sex.

Prior to the time when cloacal characters are most important for aging (8 months of age or less), the possession of tail feathers with notched tips serves to identify the juvenile component of a population. Juveniles of both sexes can be identified up until March 1 by the presence of two or more notched tail feathers (outer pair does not show notching), whereas all older geese have tail feathers with entire tips. During the autumn and winter months there is a gradual outward moult of the tail feathers beginning with the central pair, and replacement by a new set that is longer, broader at the tip, and which does not become notched from abrasion. A few juveniles may have replaced all but 2 to 4 of their juvenile tail feathers, but usually several of the new rectrices are only partially develcped and are indicative of the age of the bird. The new tail feathers are more glossy and are blacker than the juvenile feathers which by winter have become relatively worn and faded.

Juvenile males can also be identified easily by the small size and undeveloped state of the penis. As Elder (1946) states, "it does not exceed 10 mm. in length, and resembles in size the exposed lead of a well sharpened pencil; it is of the same pink color as the cloaca wall" (Plate 3, *B*). Elder's paper should be consulted for detailed information regarding age criteria in juveniles.

Bursa of Fabricius. This investigator's findings on bursal depths in Canada geese at various ages agree in general with those of Elder (1946), but differ in respect to the amount of variation found. Because all measurements presented here were taken from live birds with use of a speculum, it is not surprising that less variation was obtained in measurement of bursal depths.

Since most attention was given to geese over one year of age, the bursas of only 17 juveniles were measured. The bursas in these individuals varied between 24 and 35 mm. and averaged 27 mm.

The bursas of 108 yearling geese were examined with the aid of a speculum. Only two of this number had bursas that seemed to be closed. In most individuals the bursa was 21 mm.-deep at time of examination (average of 46 individuals, 20.5 mm.) and the variation in bursal depth was from 18 to 24 mm.

Bursa studies were made of 65 geese approximately two and one-half years old (in their third winter of life). Thirty-eight (58 per cent) of these individuals had closed bursas, while, in the remaining 27 (42 per cent), the bursa was open. The average depth of the bursa of 20 of the latter geese was 15 mm. and the extremes were 7 and 21 mm. If the 38 birds having closed bursas are averaged with those having an open bursa, the average bursal depth of all geese in their third winter is 5 mm.

The opening into the bursa in these older geese is seldom marked by the presence of prominent fleshy lips as in

the case of younger geese. Instead, the site of the opening is generally flush with the walls of the proctodeum, and is often more difficult to probe. In some individuals, normal exploration with the probe indicates a closed bursa, but with slight added pressure the probe may penetrate the bursa 5 to 18 mm. In such cases one gains the definite impression that the opening or the walls of the bursa remnant had started to grow together and that the probe pierced this original adhesion.

Absorption of the bursa may be quite rapid in some individuals in their third year; the bursa of two geese probed showed a regression of 10 mm. within a one-month period: January 22, bursa 20 mm.; February 14, bursa 10 mm.; January 24, bursa 20 mm.; February 14 bursa 10 mm.

In five geese which were three and one-half years old the bursa was closed, while in 37 geese of mixed ages, but whose *minimum* age was three and one-half years, only two geese were recorded as having an open bursa. The bursal depth in these two individuals was not recorded.

The presence of a bursa of Fabricius is generally associated with sexual immaturity, although as Kirkpatrick (1944) points out, in the case of the ring-necked pheasant, involution sometimes proceeds prior to attainment of maturity. Thus, we might expect, as is actually the case, a much longer persistence of this organ in such a relatively slow maturing bird as the Canada goose.

As a criterion of age in Canada geese, the bursa is chiefly of value in identifying yearling males, but it must be used in combination with other cloacal characters. The absence of a bursa, as indicated by probing, may be considered quite certain evidence that a goose is at least two and one-half years old.

The penis and naked area. Elder (1946) indicated that the penis is of little value in distinguishing Canada geese in their second winter from older birds. It is not clear, however, from his paper whether his opinion is based chiefly on

TABLE 1.—CRITERIA OF AGE IN JUVENILE, YEARLING ADULT AND OLDER ADULT CANADA GEESE

Criteria	Juveniles		Yearling Adults		Older Adults	
	Males	Females	Males	Females	Males	Females
Tail feathers	Notched	Notched	Tips entire	Tips entire	Tips entire	Tips entire
Bursa	Open	Open	Open	Open	Open in 42% of 2½ year old geese, closed in older geese	Open in 42% of 2½ year old geese, closed in older geese
Average depth	27 mm.	27 mm.	20.5 mm.	20.5 mm.	15 mm. in 2½ year old geese	15 mm. in 2½ year old geese
Variation	24–35 mm.	24–35 mm.	18–24 mm.	18–24 mm.	7–21 mm. in 2½ year old geese	7–21 mm. in 2½ year old geese
Naked Area	Usually pinkish red	Usually pinkish red	Usually Pinkish red	Usually Pinkish red	Flesh red to purple	Flesh red to purple
Penis	Not sheathed or coiled, less than 10 mm. in length, pink in color	—	Sheathed and coiled, typically about 10 mm. long and 4 mm. in diameter unextended, sheath pale flesh in color, turgid in appearance	—	Sheathed, unextended is *50–100%* larger than typical yearling, prominent venation, dark red to purple in color, usually flaccid in appearance	—
Oviduct	—	Closed	—	Closed	—	Open

the examination of captive or wild birds, the former possibly being slower to mature. This investigator believes that penis characters, when considered together with the bursa, are quite useful in classifying the age of the majority of the males. This opinion is based on records of 160 yearling and older geese in the autumn and winter period. For the sake of convenience in later analyses, these birds were divided into six different categories according to the relative size and appearance of the penis, and the color of both the anal sphincter muscle and the penis. These categories can be reduced to two for the purpose of simplicity.

The naked area covering the anal sphincter muscle of the typical yearling male is a pale flesh red. The penis, sheathed and unextended, is about 10 mm. long and 4 mm. in diameter. Perhaps the most characteristic feature of the penis in yearling geese in the winter is the pale, translucent color and smooth appearance of the skin of the sheath which gives the organ a rather turgid appearance (Plate 3, *C* and *D*).

The naked area of older geese is usually a darker red or of varying hues of purple. The sheathed and unextended penis of older geese is generally half again to twice as large as the organ of typical yearlings. The sheath itself is usually darker red in color than in the case of yearlings and is sometimes tinged with purple, particularly toward the distal end. The skin of the sheath has the appearance of being wrinkled, and sub-cutaneous venation is more prominent (Plate 3, *E* and *F*).

It must be understood that the above descriptions apply to best advantage only to geese during the autumn and in winter to about February 1; that the differences between cloacal characters of yearling and older males are relative; and that some experience is needed before it is possible to distinguish between these two age groups.

On the basis of the penis characters alone, 14 males out of 87 of known age (74 geese one and one-half years old and 13 geese two and one-half years old, the two age classes most likely to be confused) would have been mistakenly aged—an error of 16 per cent. However, this criterion of age considered together with the bursa would reduce the per cent of error somewhat. The error in aging all male geese over one and one-half years of age is less than 16 per cent (about 11 per cent) since the normal component of males in the population that are three and one-half or more years of age must be taken into consideration. This group is readily recognized since with few exceptions the bursa is completely closed. Consequently, the over-all error in separating yearling males from older males on the basis of characters described above will probably lie somewhere between 10 and 15 per cent.

The oviduct. The presence or absence of an occluding membrane over the opening of the oviduct is the most useful character for separating yearling female Canada geese from older females. Of a recorded sample of 54 yearling females, all possessed an occluded oviduct, whereas all but one out of 18 females that were two and one-half years of age had an open oviduct. When the catch of older females is added to the total number of yearling and two and one-half year old females examined, the error in separating yearling from

older females is about one per cent. Many other two and one-half year old females were examined for which data regarding the condition of the oviduct were not recorded. No other instance of a female two and one-half or more years of age still possessing a closed oviduct was encountered.

MALLARD AND PINTAIL

In ducks that mature at the age of one year, separation of the breeding adults from the birds of the year is a relatively simple matter. For ducks that mature at more than one year of age, the goldeneye, bufflehead, old squaw, harlequin, scoters, eiders (from Hochbaum, 1942), and the American merganser, there is again the problem of recognizing the non-breeding yearlings if the size of the breeding component in any population is to be known. Presumably the yearlings of these species would possess at least some of the criteria of age that would parallel those described for yearlings in Canada geese.

In the case of mallards (*Anas P. platyrhynchos*) and pintails (*Dafila acuta tzitzihoa*), that breed the first spring following hatching, there are only two age classes that are important to identify in the autumn—the juveniles and the older breeding adults. Because the juveniles cannot be consistently identified in the autumn and early winter by the possession of notched tail feathers, these characteristic rectrices often being moulted before mid-autumn, the cloaca must be relied upon to identify their age.

In the autumn and early winter all male mallards and pintails can be identified as to whether they are juveniles (birds of the year) or adults by the development of the penis (Hochbaum, 1942). Females, however, cannot be aged with certainty by any cloacal characters which are readily apparent when the cloaca is everted with digital pressure. Although the bursa is an accurate criterion of age through December (Hochbaum, 1942), the difficulty of probing it in live birds, as well as the time consumed in using an anesthetic, has heretofore ruled out the use of this criterion as a practical means of aging large numbers of trapped ducks. The use of a speculum fulfills the need of an extremely fast and highly accurate method for aging female mallards and pintails and presumably all other ducks that mature in one year.

Hochbaum (1942) has found that an occluding membrane over the opening of the oviduct persists in young hens (species not stated) at least through December. Inspection of the cloaca with a speculum and probe to determine the condition of the oviduct is therefore the most efficient method of aging this sex group.

DISCUSSION

At the present time Canada geese may be divided into 3 age categories in the autumn and early winter, namely: juveniles, yearling adults, and older adults. Criteria that identify these age groups are summarized in Table 1.

From the standpoint of analyses of productivity from trap catches of flying birds, there is need for criteria by which non-productive female Canada geese $2\frac{1}{2}$ years of age can be distinguished from other females of the same age that may have produced eggs the previous spring. Preliminary studies at Horseshoe Lake of the cloaca and ovaries of a number of

sacrificed birds of known age, suggest that not all females lay eggs their third spring of life. There was some evidence suggesting that the condition of the opening of the oviduct, as determined with the use of a speculum, may be a clue to the reproductive history of live individuals.

It is possible that a nasal speculum can be used to advantage in sexing and aging game birds other than waterfowl. The site at which the oviduct opens into the cloaca in immature waterfowl is marked by two small papillae. Lack of these papillae in lieu of an open oviduct would serve to indicate that the bird in question was a male. Immature females of other game birds may possess papillae or some other feature which would serve to indicate the juncture of the oviduct with the cloaca. In that event it would be possible to recognize three age and sex classes on the basis of cloacal criteria: juvenile females; adult females; and males of all ages collectively.

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THE EFFECT OF SPRING MUSKRAT TRAPPING ON WATERFOWL IN MAINE[1]

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Waterfowl investigational work has been conducted at the Maine Cooperative Wildlife Research Unit since the spring of 1938. From that date until 1947, a total of 127 ducks which were taken during the spring in muskrat traps in various parts of the State have been received at the Unit from game wardens and interested cooperators. It has been increasingly apparent that this loss might easily be of considerable magnitude since it is operating directly against breeding birds—those which have survived the shooting season and have managed to elude predators, the elements, and other mortality factors throughout the fall and winter. Mortality to waterfowl in the spring is especially serious since it is only a matter of weeks until the female would bring off her young.

Until the last two years no opportunity was afforded to measure these losses accurately but the inauguration of a muskrat project by the writer in 1946

[1] Contribution from Maine Cooperative Wildlife Research Unit, Orono, Maine; Maine Department of Inland Fisheries and Game, University of Maine, Wildlife Management Institute, and U. S. Fish and Wildlife Service, cooperating. Appreciation is expressed to Howard L. Mendall, Unit Leader, who assisted in collecting and compiling the data; to various members of the Unit personnel and to the trappers and wardens who cooperated; and the game departments of the various states and provinces that supplied information as to trapping seasons.

made it possible to work directly with the trappers and thus obtain quantitative information on the subject. In addition to the more generalized material, specific data were obtained on 6 study areas in central and eastern Maine during the spring trapping seasons of 1946 and 1947. Some of these areas were utilized heavily by waterfowl and others received only slight usage. These 6 waterways are believed to represent conditions which are quite typical of muskrat areas throughout the State as a whole. The samples are small and future findings will probably alter the results to a certain degree, but in view of the present unsatisfactory waterfowl situation it seems desirable to submit the available information at this time as a preliminary report. It is hoped that investigators in other areas may become interested in the problem and gather data so that a more complete evaluation of the losses can be made.

WATERFOWL MORTALITY IN MAINE

A compilation of data from the 127 ducks obtained from all parts of Maine is given in Table 1. Black ducks (*Anas rubripes*) comprised 43 per cent; wood ducks (*Aix sponsa*) nearly 27 per cent, and green-winged teal (*Nettion carolinense*) about 12 per cent; of other species taken, only ring-necked ducks (*Nyroca collaris*) and hooded mergansers (*Lophodytes cucullatus*) were in significant numbers. The sex ratio for all species was 105.3 males:100 females but there were some interesting variations. The black duck ratio was nearly even as was that of the green-winged teal; in contrast the wood duck ratio was 418.1 males:100 females. On the other hand, females greatly predominated among trapped ring-necked ducks and hooded mergansers where ratios of 37.5 males: 100 females and 25 males:100 females, respectively, were noted. Such variations in sex ratios of muskrat-trapped ducks are probably subject to several factors including differentials in time of the courtship behavior and degree of pairing during migration, weather influences, and the normal sex ratio of the species.

During the trapping season of 1947 a total of 30 ducks was taken in muskrat traps from three central-Maine study areas. Fourteen of the birds (about 47 per cent) were dead when found, while 16 (53 per cent) were alive and subsequently released. Of those released, 3 (19 per cent) had the leg amputated at the joint above the bare part (anatomically the ankle joint); 2 (12.5 per cent) had the foot amputated; 1 (6 per cent) had the toes amputated; 4 (25 per cent) had leg and foot bones dislocated or broken; and 6 (37.5 per cent) were damaged to an undetermined extent. No cognizance was given to birds which by their struggles and the time spent in the traps, had become soaked—on a cold day such a condition could be as deadly as if the birds were drowned. From the foregoing it can be seen that even if all birds that are found alive in muskrat traps are released, they suffer a variety of injuries, the final result of which is still a matter of conjecture. It may be surmised that any trapped bird, regardless of whether or not it is injured, will be thrown off its normal breeding schedule perhaps for the entire season. Moreover, it is likely that those ducks which lose parts of their legs, even if they survive, will not nest

TABLE 1.—WATERFOWL KILLED IN MUSKRAT TRAPS, 1938–1947 INCLUSIVE
(Statewide)

Species	Male		Female		Unsexed	Total	Per cent
	No.	Per cent	No.	Per cent			
Black Ducks (*A. rubripes*)	24	*48.0*	26	*52.0*	5	55	*43.3*
Wood Ducks (*A. sponsa*)	25	*80.7*	6	*19.3*	3	34	*26.8*
Green-winged Teal (*N. carolinense*)	7	*46.7*	8	*53.3*	—	15	*11.8*
Ring-necked Ducks (*N. collaris*)	3	*27.3*	8	*72.7*	—	11	*8.7*
Hooded Mergansers (*L. cucullatus*)	2	*20.0*	8	*80.0*	—	10	*7.8*
Blue-winged Teal (*Querquedula discors*)	—	—	1	*100.0*	—	1	*0.8*
Pintail (*Dafila acuta*)	—	—	1	*100.0*	—	1	*0.8*
Total	61	*51.3*	58	*48.7*	8	127	*100.0*

until the following year. The muskrat trapping season includes the early duck nesting period as well as the migration and hence it is especially destructive—two black ducks actually laid eggs while in traps, and in several cases birds which were examined in the laboratory were found to be laying or incubating females.

The total numerical loss of waterfowl due to spring trapping in Maine is a subject for conjecture, but by correlating the number of trapped muskrats to ducks killed in traps on the 6 representative sample areas these data can be projected for the entire State and at least give a rough approximation of the seriousness of the losses. The annual fur harvest, tabulated each year by the Department of Inland Fisheries and Game, is based on a voluntary report by each trapper when he applies for a new license and is, therefore, about one year late. The figure thus obtained is admittedly inaccurate and most people including State game officials believe it is less than the total catch; therefore, the total figure presented is considered to be conservative. The proportion of muskrats and waterfowl trapped on the study areas in the central and eastern part of the State during the two years was reasonably close. The data are as follows:

Year	*No. Muskrats Caught*	*No. Ducks Killed*	*No. Muskrats Per Duck*
1946	279	19	14.7
1947	460	26	17.7

Data for the muskrat take only in 1946 are available at this time. It is reported as being 28,594 animals. If this figure is divided by 279, the number of muskrats from the study areas in 1946, it reveals that the sample made up about 1 per cent of the total catch. This is not so large a sample as would be desired but it is believed to be a representative one and should give reasonably accurate information.

In 1946, 14.7 muskrats were caught for each duck killed; if the total muskrat catch of 28,594 animals is divided by 14.7, the result is 1,945—the number

of waterfowl taken in spring muskrat traps in Maine. At first glance this figure might not appear to be of especially significant proportions; however, when it is considered that these are breeding birds which are just about to nest or are already doing so, a far more serious situation is revealed. The figure 1,945 represents only the dead birds, 47 per cent of the trapped population; the fate of the other 53 per cent of the trapped birds (in proportion these would total 2,220 individuals) which are released is unknown. Many no doubt live but whether they reproduce and rear their young the year they were trapped is a debatable question. Thus it may be seen that at least 4,165 ducks are estimated to be affected in varying degrees as a result of being caught in muskrat traps.

Muskrat Trap Sites. An analysis of 826 spring muskrat trap sites revealed that log or plank sites formed 55.8 per cent; food platforms comprised 32.3 per cent; spots where the animals had dug 6.3 per cent; runways 2.1 per cent; stumps and trees 1.6 per cent; holes 1.2 per cent; and miscellaneous 0.7 per cent. Trap sites where 24 ducks were taken consisted of logs or planks 70.0 per cent; food platforms 20.0 per cent; and stumps or trees 10.0 per cent.

Selectivity of Muskrat Trapping on Waterfowl Species. For several years it was apparent that certain species of ducks were being taken more frequently in muskrat traps than others. For example, in Table 1 it may be noted that black ducks formed 43 per cent of the birds received and wood ducks about 27 per cent, but not a single goldeneye (*Glaucionetta*) was recorded. This brought up the question: Are the various species being taken in the same proportion as their abundance or are certain species more susceptible to trapping than others? The type of habitat determines to a great degree the species of ducks present and will result in more of such favored ones being taken. For instance, on one of the study areas the entire group of trapped birds consisted of black ducks, while on another wood ducks predominated. From available information it appears that surface feeding ducks are generally more susceptible than the diving ducks to muskrat trapping. The former frequent the water edges where muskrat traps are most likely to be set while the diving birds generally find open water areas more to their liking. Among the surface feeding ducks the breeding habits and general characteristics are probably responsible for the variation by species in mortality.

WATERFOWL MORTALITY IN THE NORTHEAST

The seriousness of spring muskrat trapping on the migrating and breeding population of ducks in Maine seems apparent. The effect of such trapping activities on the waterfowl population of the entire northeastern part of North America is another matter. The sample in Maine is much too small to attempt to project the data over this vast territory. Variations in trapping techniques and different habitat conditions and the trapping pressure are only a few of the variables to contend with. Hagar (1946) in speaking of spring and summer recoveries of black ducks reports the following: "The Hermitage Bay record leads directly into an interesting aspect of spring and summer recoveries—the method of capture. Of the 113 spring

and summer recoveries, 47 were reported as 'caught in muskrat traps.' A dozen more from the same localities and at corresponding dates were 'captured,' 'taken,' or 'found dead,' all of which terms are probably euphemisms for the first. Adding to these some part of the 27 birds for whose death no cause was given, it appears that upward of 70 per cent of the spring recoveries were the result of muskrat trapping. . . . Muskrat traps catch the greatest number of Blacks, in New Brunswick (22 out of 27), Maine (6 out of 8), and Newfoundland (14 out of 28)."

Thus it is apparent that waterfowl losses result from spring muskrat trapping over a large part of the northeast. Table 2 shows the current seasons for the taking of muskrats in those states and provinces forming the major part of the known black duck breeding range. This information is up to date as of February, 1948.

From the Table it is apparent that spring trapping is widespread over the major part of the black duck breeding range. Of the 22 states and provinces listed a total of 15 have at least part of their muskrat trapping season in the spring. If the mortality in other states and provinces is proportionate to that in Maine, loss of breeding waterfowl due to spring muskrat trapping could easily be of major importance over this vast area.

TABLE 2.—MUSKRAT TRAPPING SEASONS WITHIN THE BLACK DUCK BREEDING RANGE

State or Province	Muskrat Trapping Season[1]	Approximate Season of Year
Delaware	Dec. 1–March 10	Winter, Spring
Maryland	Jan. 1–March 15	Winter, Spring
New Jersey	Dec. 1–March 15	Winter, Spring
Pennsylvania	Dec. 1–Feb. 1	Winter
New York	Jan. 1–April 20	Winter, Spring
Connecticut	Nov. 1–March 31	Fall, Winter, Spring
Rhode Island	Nov. 1–March 1	Fall, Winter, Spring
Massachusetts	Nov. 1–March 1	Fall, Winter, Spring
Vermont	Oct. 25–April 19	Fall, Winter, Spring
New Hampshire	Oct. 20–Feb. 1	Fall, Winter
Maine	Nov. 17–30 & March 20–May 15	Fall, Spring
Ohio	Nov. 15–Jan. 15	Fall, Winter
Michigan	Nov. 1–Dec. 31	Fall, Winter
Wisconsin	Oct. 25–March 15[2]	Fall, Winter, Spring
Minnesota	Dec. 1–Dec. 10	Winter
Ontario	Feb. 11–May 31	Winter, Spring
Quebec	Nov. 1–20 & March 15–May 14	Fall, Spring
New Brunswick	April 1–May 25	Spring
Nova Scotia	Nov. 1–Dec. 15	Fall, Winter
Newfoundland	Nov. 1–May 30	Fall, Winter, Spring
Labrador	Information not available	
Prince Edward Island	Nov. 1–March 31	Fall, Winter, Spring

[1] The dates as listed are not intended to imply that muskrat trapping is permitted throughout the state or province during the entire season. Many states and provinces are subdivided so that some areas will be closed while others are open. However, the periods given indicate that some sections of each state or province are open to trapping between the inclusive dates.

[2] October 25 to January 1 (water sets permitted): January 2 to March 15 (water sets prohibited).

SUMMARY

1. A total of 127 ducks that had been caught in muskrat traps were received at the Maine Cooperative Wildlife Research Unit from 1938 to 1947. These consisted of 43 per cent black ducks, 27 per cent wood ducks, 12 per cent green-winged teal, 9 per cent ring-necked ducks, and 8 per cent hooded mergansers; other species were of little significance. The sex ratio of all species was 105 males:100 females. Wood ducks were predominately males while the ring-necked ducks and hooded mergansers were largely females; other species were more equally divided as to sex.

2. Quantitative data were obtained on 6 study areas in central and eastern Maine in 1946 and 1947. In 1946 a ratio of 14.7 muskrats trapped to each duck was obtained—in 1947 it was 17.7 muskrats per duck.

3. The total kill of ducks in muskrat traps in 1946 for Maine was conservatively estimated as 1,945 birds. In addition an estimated 2,220 birds were trapped and released alive, suffering various degrees of injury. These figures assume greater importance when it is considered that they were birds already in, or approaching, the breeding cycle.

4. Muskrat trap sites on logs or planks were used most often; they also caught the most ducks.

5. Muskrat trapping is selective in its effects on waterfowl both as to species and as to groups. As a rule, diving ducks were less susceptible to trapping losses than surface feeding ducks.

6. Spring muskrat trapping seasons are in effect in at least 15 of the 22 states and provinces that constitute the major part of the known black duck breeding range. If the waterfowl mortality over this vast area is proportionate to that in Maine, the combined losses are of serious concern.

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RUFFED GROUSE POPULATIONS IN MINNESOTA IN RELATION TO BLOOD AND INTESTINAL PARASITISM[1]

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Ruffed grouse populations reached a peak in Minnesota in 1941–42. Kill figures for the fall hunting season of 1941 were 384,000 birds, and the 1942 spring census (King's Method) on five areas showed a population of one grouse to 5.8 acres. Populations held up well during the October open season of 1942,

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(361,500 birds were harvested), but a census of the five areas made in December of that year revealed that grouse had all but disappeared from two of these areas—one at Grand Marais in extreme northeastern Minnesota and the other in the Cloquet Valley Forest north of Duluth. On the other areas populations had fallen noticeably. This was the beginning of the grouse decline in Minnesota. Gradually it spread westward. The 1943 spring census of the five areas gave a population of one grouse to 25.4 acres and the kill that autumn was 171,178 birds. In 1944, in the western part of the state, there were still shootable grouse populations near Itasca State Park. But by spring 1946, few birds remained there.

The recovery phase of the cycle began in 1947 and was most evident near Grand Marais where birds first began to disappear in 1942.

At the peak of the grouse numbers in 1941, we began a study of blood and intestinal parasitism in relation to population fluctuations which we planned to conduct for 10 years. Seven years have now elapsed and some information has been accumulated. But less than we had hoped for. The war intervened, and ever-diminishing grouse populations made it more and more difficult to obtain birds. While we would like to continue this study for another three years, we believe that the time has come for evaluating and presenting the data already assembled.

Collection of Grouse, Brood Counts, and Preparation of Material

Grouse were collected and brood counts made once and sometimes twice a year, usually in July when the young were three to four weeks old and again in September when they were almost mature. Some blood slides and intestinal tracts were obtained during open grouse seasons in 1942 and 1943. Miles driven on collecting trips and size of broods for various years are given in Table 1. The figures indicate the downward trend of grouse reproduction from 1942–46 and the beginning of recovery in 1947.

Table 1.—Number of Miles Driven on Grouse Collecting Trips, Coveys Seen, and Average Size of Coveys

Year	Miles of Driving	Coveys Seen	Ave. No. Birds Per Covey
1942	1,903	20	4.5
1943	2,335	4	7.7
1944	2,301	2	9.0
1945	722	0	0.0
1946	787	0	0.0
1947	2,560	9	7.2

On collecting trips gravel roads and other little-traveled roads were driven at all hours of the day, but especially morning and evening hours. Speeds of 15 to 20 miles per hour enabled us to watch the roadsides and road ahead for grouse. Whenever a bird or a covey appeared, we stopped quickly and shot one or two birds from the covey. As the birds flushed to the sound of the shots, the covey size was determined.

Dead grouse, we soon discovered, are almost as difficult to get blood out of as turnips. Even though we rushed to a fallen bird, it was frequently impossible to get enough blood for a smear unless we opened the pleural cavity. Two slides were smeared from each bird. The digestive tracts were removed along with heart, lungs, liver, and spleen. All

were tied in cheese cloth and preserved in formalin. Birds were sexed and age determined by the presence or absence of the Bursa of Fabricius.

In the laboratory, intestinal contents were removed and washed through sieves (400 meshes per cm.^{2}) which retained all worms. Material remaining in the sieves was examined in a black pan and the worms removed for identification. Worms were cleared in lacto-phenol for study or stained with borax carmine and then cleared in beechwood creosote. Blood slides were stained with Wright's stain and examined for at least 15 minutes before they were pronounced negative for *Leucocytozoon bonasae*.

During the seven-year period, 1941–1947, a total of 231 grouse was examined for intestinal parasites. Blood slides were obtained from 163 of these birds. Immature birds, some of them three to six weeks old, were collected as well as adults in order to determine the variations of infestations in the age classes. Variations of infestation were studied, too, from the standpoint of geographical origin of the birds. The northeastern part of their range, north and east of Lake Superior, was designated as Zone I, the northwestern part of the range west and north of Cass Lake, as Zone II, and the area between as Zone III. These zones were first used by Boughton (1937) in his study of grouse parasites and are based on meteoro-topographical conditions. The data on age classes and sexes of ruffed grouse and on numbers collected in the various zones are summarized in Table 2.

TABLE 2.—AGE AND SEX OF RUFFED GROUSE, AND NUMBERS COLLECTED IN VARIOUS ZONES, 1941–1947

Year	Total Birds	No. of Adults Examined	No. of Young Examined	Age Unknown	Male	Female	Sex Unknown	Zone I	Zone II	Zone III
1941	47	12	25	10	27	16	4	2	6	39
1942	83	33	50	0	35	47	1	34	19	30
1943	33	23	10	0	21	7	5	20	0	13
1944	40	15	25	0	20	16	4	8	17	15
1945	5	1	4	0	3	2	0	4	1	0
1946	4	3	1	0	2	2	0	4	0	0
1947	19	3	16	0	12	5	2	19	0	0
Total	231	90	131	10	120	95	16	91	43	97

BLOOD PARASITES

Of the 30-odd protozoan and helminth parasites reported from ruffed grouse, the blood protozoon, *Leucocytozoon bonasae*, has been considered the one most likely to be important in influencing cyclic fluctuations of these birds. Clarke (1936) in his study of cyclic fluctuations of ruffed grouse in Ontario, concluded that infection by this organism was the only factor that he could positively correlate with declining grouse populations.

It is well known that infections of *L. simondi* in ducks and *L. smithi* in turkeys are highly fatal to young birds. Black flies (*Simulium venustum* and *S. nigroparvum*) serve as vectors for the *Leucocytozoon* of ducks and turkeys, and

the sexual proliferation (gametogenesis) of the organism takes place in these flies. It was not until 1946 that Fallis and Davies proved that *L. bonasae* of grouse is also spread by the bites of black flies although this had been long suspected.

What effect *L. bonasae* has on immature ruffed grouse is not known. And this is not surprising since capturing infected birds and maintaining them in the laboratory is at best difficult. Blood from an infected adult grouse held in the laboratory for several weeks, was injected into baby chicks with negative results. This bird was finally sacrificed. Tissue sections of its liver showed many *Leucocytozoon* organisms multiplying in the hepatic cells and a noticeable amount of tissue pigment, melanin, in the cytoplasm of the liver cells. These conditions are definite evidence of liver damage caused by *L. bonasae*.

Leucocytozoon organisms are known to leave the peripheral blood in winter and retreat to the liver, spleen and bone marrow. We have found gametocytes in the blood as late as November 15.

The percentages of *Leucocytozoon* infections have been large during six of the seven years when specimens were obtained (Table 3). No blood slides were made in 1946. In 1941, 63.3 per cent of the birds were infected; in 1942, when the die-off started in the northeast (Zone I), 61.2 per cent were positive. The next year the infection reached a peak when 83.3 per cent of the birds were parasitized, and then dropped back to 59.4 per cent in 1944. In 1947, when grouse were definitely on the increase, 100 per cent of the 19 birds examined were infected.

TABLE 3.—INFECTIONS OF *Leucocytozoon bonasae* IN RUFFED GROUSE, 1941–1947

Year	No. Birds Examined	No. Birds Infected	Per Cent Infected
1941	30	19	*63.3*
1942	49	30	*61.2*
1943	30	25	*83.3*
1944	32	19	*59.4*
1945	3	3	*100.0*
1947	19	19	*100.0*
Total	163	115	*70.5*

This phenomenon of increased parasitism of a cyclic species well out of the doldrums and on its way to population recovery may be characteristic of the initial portion of the recovery period. Erickson (1944) found this to be true of the snowshoe hare and suggested that parasites (helminths in this case) may be secondarily cyclic with the decline in numbers lagging behind the host recovery. If this is the case and if parasites are one factor influencing cyclic fluctuations, which we believe to be true, then further blood studies of grouse should show decreased *Leucocytozoon* infections.

Immature ruffed grouse less than one year old, according to our studies, are more apt to show infections of *L. bonasae* than are adult birds. Several factors undoubtedly are at work to produce this condition. For example, it is possible that immature grouse are more susceptible to infection than adults, that adults because of previous infection have developed resistance to reinfection, and that the *Leucocytozoon* in adults is more apt to be confined to the reticulo-endothelial system than it is in immature birds.

Table 4 summarizes the infections in immature and adult birds for the seven-year period. Eighty-two of 114 immatures (71.9 per cent) were positive

for *L. bonasae;* 33 of 49 adults (67.3 per cent) were positive. In only two of the years, 1942 and 1947, were percentages of infection identical for both age classes.

Not enough grouse were collected in all three zones each year for comparison of infections by zones. The information available, however, for 1942, 1943, and 1944 shows that the percentage of infected birds in the various zones in any one year differed slightly. The total percentage of infection in the three zones for the six years was Zone I, 75.6; Zone II, 64.7; and Zone III, 65.2.

Table 4.—Infections of Leucocytozoon bonasae in Ruffed Grouse by Age Classes

Year	No. Immatures Examined	No. Infected	Per cent Infected	No. Adults Examined	No. Infected	Per cent Infected
1941	26	17	*65.4*	4	2	*50.0*
1942	36	22	*61.1*	13	8	*61.5*
1943	9	8	*88.8*	21	17	*80.9*
1944	24	16	*66.6*	8	3	*37.5*
1945	3	3	*100.0*	—	—	—
1947	16	16	*100.0*	3	3	*100.0*
Total	114	82	*71.9*	49	33	*67.3*

Although *L. bonasae* was the most common blood parasite of the grouse examined, two others occurred sporadically, *Trypanosoma* sp., and a *Microfilaria*. Percentages of infection by these species are given in Table 5.

Examination of Chicken Blood

Domestic fowl harbor many parasites. Might they not be parasitized by *L. bonasae*, and if so could they not serve as a reservoir of the infection when grouse become so scarce that even the black flies cannot find them? So we reasoned in 1944, and thus came to collect blood from 47 chickens in 14 localities in northern Minnesota. None of these birds, however, was infected, nor do we know of any positive records of *Leurocytozoon* infection in Minnesota domestic fowl.

Intestinal Parasites of Grouse

Food habits of the host have much to do with the kinds of parasites harbored by the host, the extent of parasitism, and the effect of the parasitism. For the first two to three weeks of life grouse, for example, live almost entirely on animal food—slugs, worms, and insects. Thus they tend to harbor parasites whose immature stages are passed in these animals. Adult grouse, on the other hand, live chiefly on vegetable foods, and have few of these parasites. They tend, in general, to harbor parasites whose life cycles are direct. The relative frequency of parasitism of the grouse examined is shown in Table 5.

Two common parasites of immature ruffed brouse encountered in this study were the tapeworms, *Davainea proglottina* and *Raillietina tetragona*. These are known to produce serious effects in bobwhite quail and chickens. It is entirely possible that they may be responsible for a part of the considerable mortality that is known to occur among

TABLE 5.—RELATIVE FREQUENCY OF PARASITES OF RUFFED GROUSE, 1941–47

Parasite	Number Examined	Number Infected	Percentage Infected	Organ
Roundworms				
Ascaridia bonasae	231	87	*37.6*	sm. intestine
Cheilospirura spinosa	231	11	*4.7*	gizzard lining
Heterakis gallinae	231	1	*0.43*	ceca
Microfilaria sp.	163	7	*4.3*	blood
Oxyspirura petrowi	203	1	*0.49*	eye
Flukes				
Brachylaemus fuscatus	231	20	*8.6*	ceca
Echinoparyphium aconiatum	231	2	*0.86*	sm. intestine
Lyperosomum monenteron	203	1	*0.49*	liver
Tapeworms				
Choanotaenia infundibulum	231	3	*1.3*	sm. intestine
Davainea proglottina	231	23	*10.0*	sm. intestine
Hymenolepis sp.	231	5	*2.1*	sm. intestine
Raillietina tetragona	231	14	*6.0*	sm. intestine
Protozoa				
Eimeria angusta	203	4	*2.0*	intestine
Eimeria bonasae	203	1	*0.49*	intestine
Leucocytozoon bonasae	163	115	*70.5*	blood
Trypanosoma sp.	163	2	*1.2*	blood

young ruffed grouse. Percentage of infection of immature and adult birds by various worm parasites are given in Table 6.

The percentage of all grouse infected by the various helminths during the seven years of this study followed no consistent pattern. In other words, there was no indication that worm infestations were building up as grouse populations were falling farther and farther into the cyclic decline. Likewise there was no indication that infestations were more severe in grouse from one zone than in grouse from another, or in immature birds collected one year against those collected in another.

The seemingly indefinite trend of worm infections year by year may have been the result of too few examinations of birds each year. Boughton (1937) showed that there was a remarkable increase in the percentage (37 per cent) of worm-infected grouse from 1931 to 1935 as the cycle of declining grouse populations progressed in its downward swing. Yet he did not believe that

TABLE 6.—RELATIVE FREQUENCY OF THE MORE COMMON WORM PARASITES OF IMMATURE AND ADULT RUFFED GROUSE, 1941–47

Parasites	Immature Birds	Number Infected	Per cent Infected	Adult Birds	Number Infected	Per cent Infected
Roundworms						
Ascaridia bonasae	133	47	*35.3*	90	39	*43.3*
Cheilospirura spinosa	133	5	*3.7*	90	6	*6.7*
Flukes						
Brachylaemus fuscatus	133	16	*12.0*	90	5	*5.5*
Tapeworms						
Davainea proglottina	133	20	*15.0*	90	3	*3.3*
Raillietina tetragona	133	14	*10.5*	90	—	—

worms were responsible for the die-off of grouse. Rather, he considered the grouse to be in excellent condition.

SUMMARY

Ruffed grouse populations reached a peak in Minnesota in 1941–42 when a study of blood and intestinal parasitism in relation to grouse fluctuations was begun.

During the seven-year period, 1941–47, 231 grouse were examined for intestinal parasites, and blood slides were obtained from 163 of these birds.

In 1941, 63.3 per cent of the grouse were infected by the blood protozoon, *Leucocytozoon bonasae;* in 1942, when the die-off of grouse started 61.2 per cent of the blood slides were positive. The next year the infection reached a peak when 83.3 per cent of the birds were parasitized. In 1947, when grouse were definitely on the increase again, 100 per cent of 19 birds examined were infected. This phenomenon of increased parasitism of a cyclic species on its way to population recovery may be characteristic of the initial portion of the recovery period. Erickson (1944) pointed this out in the case of the snowshoe hare. Immature ruffed grouse are more apt to show infections of *L. bonasae* than are adult birds. During the seven-year period 82 of 114 immatures (72 per cent) were positive for *L. bonasae:* 33 of 49 adults (67.3 per cent) were positive.

Although 12 species of helminths were recovered from the 231 birds, only five occurred with any degree of regularity: roundworms, *Ascaridia bonasae* and *Cheilospirura spinosa;* flukes, *Brachylaemus fuscatus;* and tapeworms, *Davainea proglottina* and *Raillietina tetragona.* The last two occurred much more frequently in immature birds than in adults.

There was no indication that worm infestations were building up as grouse populations were declining The seemingly indefinite trend of worm infections year by year may have been the result of too few examinations each year.

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TOOTH DEVELOPMENT AND WEAR AS CRITERIA OF AGE IN WHITE-TAILED DEER[1]

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Knowledge of the age class composition of a game population is often essential to proper management. This is especially true with respect to the annual replenishment of young stock, which must at least equal the total losses of adults if a population is to remain stable, or must exceed them if it is to increase. By knowing the proportions of the various age classes among the adults present one may determine the average life-span as well as the slope of the survival curve throughout the years represented. Once the normal pattern of these relationships has been learned, deviations can be recognized which might be corrected through adjustments of hunting regulations or which might indicate opportunities for other forms of management.

The need for information of this kind for the white-tailed deer (*Odocoileus virginianus*) in New York became evident several years ago. Related problems in this case were the extent to which winter mortality might involve late-born fawns and the age of adult deer found dead in wintering areas. Existing data on age composition based on tooth conditions described by Cahalane (1932) showed that the heaviest winter losses were among fawns, secondly among old deer and lowest among deer of prime age. The ratio of dead fawns to dead adult deer varied with the severity of the winter. With these indications it was suggested that if a reliable method of aging deer could be found, a study of the age composition of the fall deer take should reflect the variations in deer losses from winterkill from year to year. If this were true further study of the fall age composition should provide needed information on the relative survival of fawns and older deer in relation to prime-aged deer.

Review of the literature indicated tooth development and wear to be the most reliable criteria of age for this species, but specific information was meager. No one had made an adequate collection of known-age material. The most important work was that of Cahalane (1932) who had attempted to correlate age with antler diameter on the basis of 244 specimens arranged according to dentition and other skull characters. Yet, of this entire series, the age of only one had been positively known.

An effort, therefore, was commenced in 1940 as a part of this project to as-

[1] A contribution from Pittman-Robertson Wildlife Restoration Projects 1-R and 28-R, New York State Conservation Department, Bureau of Fish and Wildlife Investigations. The author is especially grateful to E. L. Cheatum, Senior Game Pathologist, and John E. Tanck, Conservation Aide, for the assistance rendered during the course of this study. The writer is also indebted to Dr. W. C. Senning, Chief Aquatic Biologist, and Robert W. Darrow, Supervisor of Game Research, for the supervision they have freely given during the study and assistance given during the preparation of the manuscript.

semble a collection of known-age deer jaws sufficient to provide the basis for a reliable index of age. In 1944, a definite study of criteria for aging deer was incorporated in the project and work was completed in 1946. This paper is the result of that work.

MATERIAL

From 1940 to 1944 only a few records were collected but many deer were tagged as fawns and in due time they provided specimens in the older age classes. These deer were held within an 87-acre enclosure 25 miles southwest of Albany. Other deer were raised at the Research Center at Delmar, and a few deer of known-age possessed by individuals at various private deer parks were given to the author.

Material collected from these sources comprised 127 age records from 81 individual deer. Fifty-six deer were examined once (56), 14 deer were examined twice (28), five deer were examined three times (15), three deer were examined four times (12), two deer were examined five times (10), and one deer was examined six times (6). Thus, a total of 67 sets of notes on tooth replacement and wear and 60 jaws were collected (Table 1). Of these, 101 were on deer of various ages from birth to two years inclusive and 26 were on deer from two years of age and older.

The 101 sets of data on deer two years old or less were derived from deer raised in pens at the Research Center. Of these, 29 were from 13 deer born at the Research Center. The other 72 sets of data were from 41 fawns that were picked up in the wild during May and June, sent to the Research Center and aged according to data derived through the study of deer born at the Center. Individual deer from both groups, born in pens and born in the wild, were reexamined at intervals in order to note changes in tooth development.

The 26 sets of data on deer above two years of age were derived from 10 deer liberated in the enclosure as fawns and allowed to feed on natural forage. Eight deer were sent in by interested individuals who had raised them on natural forage and the other eight deer were raised from fawns and never left the pens at the Research Center.

METHODS

Deer used in this study, except those from private parks, were marked with numbered ear-tags as they became available to the study. Fawns born at the Research Center, hereafter referred to as "known-age specimens," were used to develop criteria for aging other fawns less than two months of age. Fawns taken from the wild and confiscated from their captors were assigned a birth-date after examining their tooth development and comparing it with the tooth condition of the known-age specimens. To check on this assigned date of birth, game protectors when confiscating fawns established the earliest date of possession. These two dates were then compared to determine any underestimation of the age of the captured fawns. Most confiscated fawns were five days old or less when captured and, because their date of birth was established by use of data from known-age fawns, they are hereafter referred to as "established-age specimens."

Subsequent examinations of live deer were made at intervals. Young fawns,

one to three weeks old, were securely held while being examined. Older deer were placed under general anaesthesia by intra-venous injection of sodium pentabarbital. The animals were completely relaxed within one to three minutes (a few older deer in very good physical condition would struggle for five minutes) and were easily handled. An abdominal retractor was used to hold the mouth open and critical examination of the teeth was facilitated by the use of a dental mirror and flashlight.

In addition to the collection of data on known- and established-age specimens, approximately 750 jaws have been collected from deer found dead in the wild. These jaws have been critically examined for abnormalities in tooth wear which might make aging difficult. They were also used to check on variations in the order of tooth replacement and whenever live deer were examined jaws from wild deer showing identical tooth replacement, development and wear were used to augment the descriptions.[2]

Age classes two years and above were first described in the spring of 1945. Since then, three specimens 2½ years old, three specimens 3½ years old, five specimens 4½ years old, two specimens 6½ years old, one specimen 7½ years old and one specimen 9½ years old have been added to the collection. In the case of each added specimen, it was aged and placed in the series before the records of birth were examined. (See Growth and Wear.)

[2] The terminology used in this paper follows that of Thompson, A. H. and M. Dewey in *Comparative Dental Anatomy*. C. V. Mosby Co., 1930.

In describing the tooth condition of young deer (Tables 1 & 2) several criteria were used. The distance between the gum line and the highest point of each tooth on the lingual side was measured in millimeters. These distances were used in the first three subclasses. The criteria of age for the two following sub-classes were changed. This was necessary because fawns began to chew cud at or about four weeks of age and wear became apparent on the second premolar at five weeks of age and at eight weeks of age on the third premolar. Consequently, measurements although recorded in the text and Table 2, did not show the growth that actually occurred. The relationship between the shoulder (at the neck) of a tooth and the gum line was used to determine further advances in premolar development.

The molar teeth, being multicuspids which erupt the anterior cusps first were used as additional criteria to the incisors and premolars in the last nine sub-classes of young deer. The number of points through the gum was used to describe the development of these teeth. At some stage of development each molar was described as having one, two or four points through the gum. By using these criteria, stages of tooth eruption were described which were intermediate to full eruption.

The development of a deciduous tooth was considered complete when it was fully erupted (m). Similarly a permanent tooth was considered fully erupted (A) when it had reached its full height above the gum. In some instances deciduous teeth were lost (O) but the permanent teeth were not in place. Other specimens had a tooth

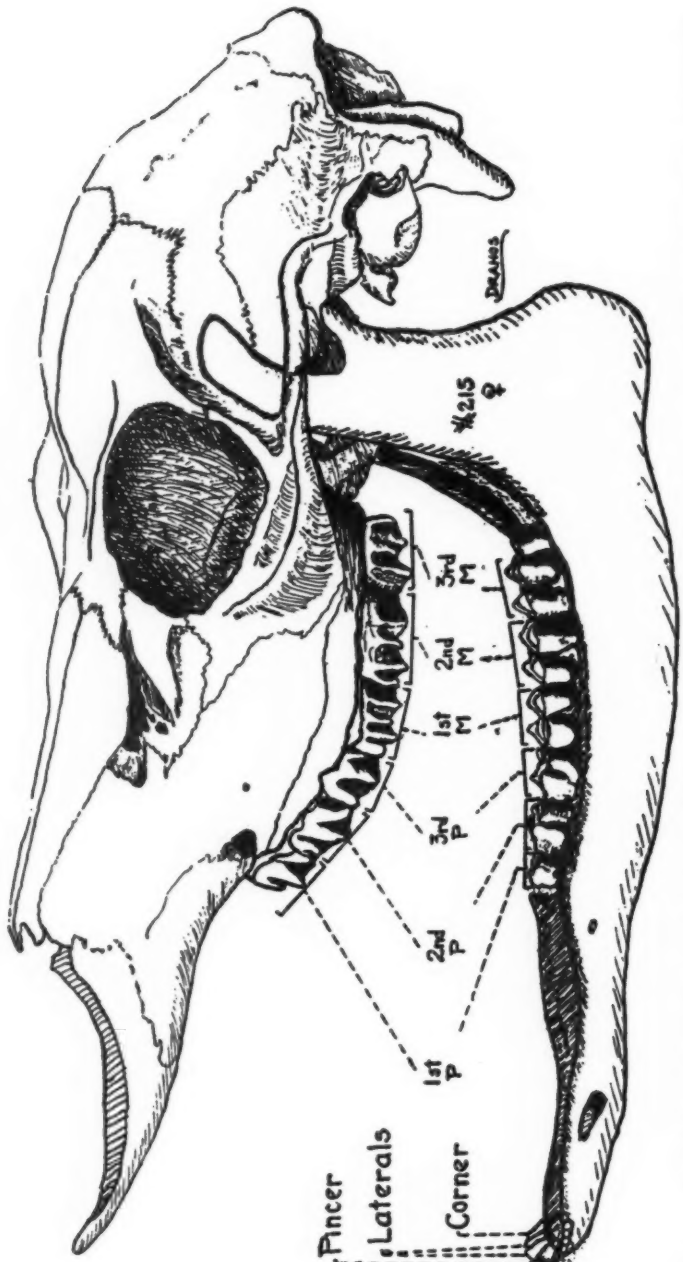

FIG. 1.—Sketch of white-tailed deer skull showing position of the various teeth referred to in text (P = premolar, M = molar).

condition in the right jaw (R) that differed from that of the left (L) and in such cases both sides were described. These various conditions are designated in Table 1 by symbols which are defined in footnotes to that table.

Describing the tooth condition of older deer (two years and above) depended largely upon a critical examination of the wear on the molar teeth primarily and secondarily on the premolars. No dependable criteria for aging older deer by the incisors were found. In addition, measurements of the height above the gum of all mandibular cheek teeth were made (Table 2). These measurements were from the highest point on the lingual crests of each tooth to the lowest point of heavy pigmentation along the gum line. On the premolars one measurement on each tooth was taken. On the first and second molars each lingual crest was measured (two on right and two on left jaw bones) and the average recorded. On the third molar each of the anterior lingual crests was measured and averaged. Because the posterior cusp of the third molar did not show growth and wear consistent with the other crests of this tooth, it was recorded separately. Figure 1 shows the arrangement and name of each tooth as they were used in this paper.

FINDINGS

The remainder of the paper will be devoted to a discussion of the data obtained and the use of tooth development and wear as criteria of age in this species.

COMPARISON OF TOOTH DEVELOPMENT IN BOTTLE-FED AND MOTHER-FED FAWNS

Early in the study a question was raised concerning differences in tooth development and replacement in deer of the same age which were bottle-fed as compared to those which were mother-fed. Differences in quality and quantity of food, shock of being shipped, proximity of humans and difficulties of acquainting them to bottle food were thought of as possible deterrents to normal growth. The author, therefore, kept records of body growth as well as tooth replacement in order to discover any differences that might exist.

Seven deer (Nos. 58, 8438, 282, 292, 295, 298 and 299)[3] were raised by their mothers. They were measured 22 different times. A comparison of their tooth development with other fawns (Table 1) showed that very little variation occurred between them and the bottle-fed fawns. Some bottle-fed fawns that apparently received poor care before being shipped to the Research Center showed a slightly retarded tooth development. On the other hand, with good care they soon regained their normal development and retained it throughout the course of the study. The author, therefore, has grouped the data from fawns raised by the two methods because any differences that did exist were very slight.

GROWTH AND WEAR OF DECIDUOUS AND PERMANENT DENTITION

Study of the growth and wear of deciduous and permanent mandibular cheek teeth of white-tailed deer indicated that a relationship between age and tooth height above the gum line did exist. Both lingual and buccal sides of these teeth were measured and, in general, the buccal measurements were one

[3] Numbers refer to project catalogue.

TABLE 1.—SUMMARY OF THE SPECIMENS USED IN THIS STUDY AND THE BASIC DATA RECORDED ON THE DEVELOPMENT AND REPLACEMENT OF THE TEETH OF WHITE-TAILED DEER FROM BIRTH TO 24 MONTHS

Age sub-class	Specimen number[a]	Sex	Type of specimen or data	Aged on date examined	Tooth development and replacement[b]		
					Incisors[c]	Premolars[d]	Molars[e]
					1 – 2 – 3 – 4	1 – 2 – 3	1 – 2 – 3 – 4[f]
Birth	215A*	F	jaw	1 day	2 – 2 – 2 – 2		
	215B*	F	jaw	1 day	2 – 0 – 2 – 2		
	104A*	F	jaw	1 day	2 – 2 – 2 – 2		
	104B*	F	jaw	1 day	2 – 2 – 2 – 2		
	1W*	M	jaw	1 day	2 – 2 – 2 – 2		
	2W*	F	jaw	1 day	2 – 2 – 2 – 2		
	298*	F	notes	1 day	2 – 2 – 2 – 2		
1 to 2 weeks	377	?	jaw	1 week	3 – 3 – 3 – 3	– 1 – 1	
	8386	F	jaw	1 week	3 – 3 – 3 – 3	– 1 – 1	
	9418	F	jaw	1 week	3 – 3 – 3 – 3	– 1 – 1	
	298*	F	notes	10 days	m – m – m – m	1 – 2 – 3	
2 to 4 weeks	291	M	notes	2 weeks	m – m – m – m	– 1 – 3	
	289	F	notes	2½ weeks	m – m – m – m	1 – 2 – 3	
	290	M	notes	2½ weeks	m – m – m – m	– 2 – 3	
	208	F	jaw	2½ weeks	(lost)	– 1 – 2	
	292*	F	notes	3 weeks	m – m – m – m	– 2 – 4	
	298*	F	notes	3 weeks	m – m – m – m	1 – 2 – 4	
	293	M	notes	3 weeks	m – m – m – m	1 – 2 – 3	
	294	F	notes	3½ weeks	3 – 3 – 3 – 3	– 1 – 2	
4 to 7 weeks	293	M	notes	5 weeks	m – m – m – m	¼ – ¼ – ¼	
	292*	F	notes	5 weeks	m – m – m – m	¼ – ¼ – ¼	
	298*	F	notes	5 weeks	m – m – m – m	¼ – ¼ – ¼	
	217	M	jaw	5 weeks	(lost)	¼ – ¼ – ¼	
	206	F	jaw	5 weeks	m – m – m – m	¼ – ¼ – ¼	
	8438*	F	jaw	40 days	m – m – m – m	¼ – ¼ – ¼	
	9551	M	jaw	6 weeks	m – m – m – m	¼ – ¼ – ¼	
	9552	M	jaw	6 weeks	m – m – m – m	¼ – ¼ – ¼	
	203	M	jaw	6 weeks	m – m – m – m	¼ – ¼ – ¼	
	294	F	notes	6 weeks	m – m – m – m	¼ – ¼ – ¼	
7 to 10 weeks	288	M	notes	7 weeks	m – m – m – m	¼ – ¼ – ¼	
	8462	M	jaw	7½ weeks	m – m – m – m	¼ – ¼ – ¼	
	298*	F	notes	8 weeks	m – m – m – m	¼ – ¼ – ¼	
	293	M	notes	8 weeks	m – m – m – m	¼ – ¼ – ¼	
	8456	M	jaw	8 weeks	m – m – m – m	¼ – ¼ – ¼	
	287	M	notes	8 weeks	m – m – m – m	¼ – ¼ – ¼	
	294	F	notes	8½ weeks	m – m – m – m	¼ – ¼ – ¼	
10 weeks to 4 months	289	F	notes	10 weeks	m – m – m – m	m – m – m	2 –
	292*	F	notes	3 months	m – m – m – m	m – m – m	2 –
	289	F	notes	3½ months	m – m – m – m	m – m – m	4 –
	299*	M	notes	3½ months	m – m – m – m	m – m – m	1 –
	288	M	notes	3½ months	m – m – m – m	m – m – m	4 –
	295*	M	notes	3½ months	m – m – m – m	m – m – m	2 –
	287	M	notes	3½ months	m – m – m – m	m – m – m	4 –
	293	M	notes	3½ months	m – m – m – m	m – m – m	4 –
4 to 6 months	282*	F	jaw	4 months	m – m – m – m	m – m – m	4 –
	289	F	notes	5 months	m – m – m – m(R) A – m – m – m(L)	m – m – m	4 –
	290	M	notes	5 months	m – m – m – m	m – m – m	4 –
	291	M	notes	5½ months	m – m – m – m	m – m – m	4 –
	287	M	notes	5½ months	A – m – m – m	m – m – m	4 –
	292*	F	notes	5½ months	m – m – m – m	m – m – m	4 –
	218	M	jaw	5½ months	m – m – m – m	m – m – m	4 –
6 to 7 months	279	M	jaw	6 months	A – m – m – m	m – m – m	4 –
	277	M	notes	6 months	A – m – m – m	m – m – m	4 – 1 –
	278	M	notes	6 months	A – m – m – m	m – m – m	4 –
	211	F	notes	6½ months	A – m – m – m	m – m – m	2 –
	280	M	notes	6½ months	A – m – m – m	m – m – m	2 –
	223	F	notes	6½ months	A – m – m – m	m – m – m	4 –
	215	F	notes	6½ months	A – m – m – m	m – m – m	4 –
	205	M	notes	6½ months	A – m – m – m	m – m – m	2 –
	58*	M	notes	6½ months	A – m – m – m	m – m – m	4 –
	219	F	notes	6½ months	A – m – m – m	m – m – m	4 –
7 to 9 months	174	M	notes	7 months	A – m – m – m	m – m – m	2 –
	173	F	notes	7 months	A – m – m – m	m – m – m	2 –
	204	F	notes	7 months	A – m – m – m	m – m – m	4 – 2 –
	299*	M	notes	7 months	A – m – m – m	m – m – m	4 – 1 –
	295*	M	notes	7 months	A – m – m – m	m – m – m	4 – 1 –
	202	F	notes	7 months	A – m – m – m	m – m – m	4 – 2 –
	225	M	jaw	7 months	A – m – m – m	m – m – m	4 – 3 –
	172	F	notes	7½ months	A – m – m – m	m – m – m	4 – 2 –
	175	M	notes	7½ months	A – m – m – m	m – m – m	4 – 1 –
9 to 11 months	278	M	jaw	9 months	A – m – m – m	m – m – m	A – 4 –
	277	M	notes	9½ months	A – m – m – m	m – m – m	4 – 2 –
	211	F	notes	9½ months	A – m – m – m	m – m – m	4 – 2 –
	295*	M	notes	9½ months	A – 0 – 0 – m(R) A – 0 – m – m(L)	m – m – m	A – 4 –

TABLE 1.—*Continued*

Age sub-class	Specimen number[a]	Sex	Type of specimen or data	Age on date examined	Tooth development and replacement[b]		
					Incisors[c]	Premolars[d]	Molars[e]
					1 – 2 – 3 – 4	1 – 2 – 3	1 – 2 – 3 – 4[f]
	299*	M	notes	9½ months	A – 0 – m – m	m – m – m	A – 4 –
	223	F	notes	9¼ months	A – A – m – m(R) A – 0 – 0 – m(L)	m – m – m	4 – 2 –
	280	M	notes	9¼ months	A – m – m – m	m – m – m	4 – 2 –
	215	F	notes	9¼ months	A – m – m – m	m – m – m	4 – 2 – (R) – 1 – (L)
	219	F	jaw	9¼ months	A – m – m – m	m – m – m	A – 4 –
	205	M	notes	9¼ months	A – m – m – m	m – m – m	A – 4 –
	202	F	notes	10 months	A – m – m – m	m – m – m	4 – 2 –
	174	M	notes	10 months	A – m – m – m	m – m – m	4 –
	204	F	notes	10 months	A – m – m – m	m – m – m	4 – 2 –
	173	F	jaw	10¼ months	A – A – m – m(R) A – A – 0 – 0(L)	m – m – m	A – 4 –
	172	F	notes	10¾ months	A – A – A – A	m – m – m	A – 4 –
11 to 13 months	175	M	notes	11 months	A – A – A – 0(R) A – 0 – 0 – m(L)	m – m – m	A – 4 – 1 –
	299*	M	notes	11 months	A – A – A – A	m – m – m	A – 4 –
	295*	M	notes	11 months	A – A – A – A	m – m – m	A – 4 –
	299*	M	notes	12 months	A – A – A – A	m – m – m	A – 4 –
	295*	M	notes	12 months	A – A – A – A	m – m – m	A – 4 –
13 to 17 months	295*	M	notes	13 months	A – A – A – A	m – m – m	A – A – 2 –
17 to 20 months	128	F	jaw	18 months	A – A – A – A	A – 0 – 0	A – A – A –
	139	M	jaw	18½ months	A – A – A – A	A – A – A	A – A – A –
	138	M	jaw	18½ months	A – A – A – A	A – A – A	A – A – A –
	145	M	jaw	18½ months	A – A – A – A	A – A – A	A – A – A –
	127	M	jaw	18½ months	A – A – A – A	m – m – m	A – A – A –
	152	M	jaw	18½ months	A – A – A – A	m – m – m	A – A – 4 –
	129	M	jaw	19 months	A – A – A – A	m – m – m	A – A – A –
	δ	M	jaw	19½ months	A – A – A – A	A – A – A	A – A – A –
20 to 24 months	277	M	jaw	23 months	A – A – A – A	A – A – A	A – A – A – A
	215	F	jaw	23 months	A – A – A – A	A – A – A	A – A – A – A

[a] Specimens designated by * born in captivity, providing positively known birth dates.
[b] For all three types of teeth, the designations "m" and "A" have been used to indicate milk and adult dentition respectively.
The designation "0" has been used to indicate where a milk tooth has dropped out, but the corresponding adult tooth has not fully erupted.
Designations "(R)" and "(L)" indicate right and left sides, respectively, of a jaw in which eruption of the teeth was not bilaterally uniform.
[c] For the incisors, numerals refer to height in mm. to which crest of tooth projects through gum.
[d] For the premolars, whole numerals refer to height in mm. to which crest of tooth projects through gum; fractions refer to the stage of development (see text under METHODS, fifth paragraph).
[e] For the molars numerals refer to the number of points projecting through gum.
[f] A separate designation "4" has been given the posterior cusp of the third molar which is relatively short and provides an added criterion for judging age between 1½ and 2½ years.

to two millimeters shorter than the lingual heights.

The data on the lingual height above the gum (Table 2) showed a rapid increase in height of the cheek teeth among young deer and a slow but continuous decrease in height of teeth of deer from maturity to old age. Similarly, these data when graphed (Figures 2 & 3) provided a good index to age of most deer but insofar as field identification was concerned, measurements were difficult to make. In addition, some individual variation in tooth size existed. Therefore, the age of a deer two years and above was most readily judged by tooth height above the gum in conjunction with the relative wear on the occlusal surfaces of the teeth.

Abnormalities in wear on the teeth of individual deer have been found. During the last two years of the study 15 specimen jaws from deer over two years of age were added to the collection (see Methods). These jaws were placed in the series of other known-age specimens before the records of birth were examined. When these records were reviewed, all but one of the 15 specimens had been properly placed accord-

TABLE 2.—AVERAGE HEIGHT IN MILLIMETERS ABOVE THE GUM LINE OF THE LINGUAL CRESTS OF THE MANDIBULAR CHEEK TEETH OF WHITE-TAILED DEER

Age Sub-class	Number of Specimens	Milk Premolars			Adult Premolars			Molars			
		1	2	3	1	2	3	1	2	3	4[a]
Birth	7	0.0	0.0	0.0							
1 to 2 wks.	4	0.3	1.2	1.5							
2 to 4 wks	8	0.4	1.6	3.9							
4 to 7 wks.	10	4.9	5.0	6.8							
7 to 10 wks.	7	4.9	5.0	5.9							
10 wks. to 4 mo.	1	5.0	5.0	6.5				2.8			
4 to 6 mo.	2	4.5	4.5	6.3				6.8			
6 to 7 mo.	1	4.5	5.0	6.0				8.5			
7 to 9 mo.	1	5.0	5.0	5.5				8.0	5.3		
9 to 11 mo.	3	5.0	5.0	5.3				9.3	6.8		
11 to 13 mo.	2	4.5	4.5	4.7				9.3	9.6		
13 to 17 mo.	1	4.5	4.5	4.7				9.5	10.5	10.5	3.5
17 to 20 mo.	8	4.3	3.3	3.3	4.6	5.5	5.8	6.9	8.9	8.1	2.8
20 to 24 mo.	2				5.2	6.5	7.0	7.0	9.0	8.6	4.8
2½ yrs.	4				5.0	6.5	7.5	7.2	8.6	9.0	4.5
3½ yrs.	3				5.3	6.1	7.3	6.8	9.1	9.0	6.0
4½ yrs.	6				5.0	5.6	6.2	6.0	7.6	8.4	6.0
5½ yrs.	3				5.3	5.3	6.0	5.7	7.2	8.0	5.7
6½ yrs.	4				4.5	4.5	6.0	4.9	6.2	6.8	4.8
7½ yrs.	3				4.7	4.7	6.0	5.0	6.3	6.7	4.0
8½ to 9½ yrs.	1				4.5	4.0	4.0	4.5	4.5	4.5	4.5
10½ years and over	2				3.0	3.0	3.5	4.2	4.5	5.2	4.5

[a] Posterior cusp of third molar.

ing to its age. The one exception was aged at four years and was actually four years and ten months old. The wear, abnormally heavy on the first molar of this specimen, approximated the condition of the same tooth in a 7½-year specimen. Therefore, in order to age this deer an average of the wear on the first molar as against the wear on the other molars and premolars had to be struck. In deriving the average, the specimen was underaged by ten months. Such abnormalities in wear have not been a great source of error. An average of only one specimen in 15 from a sample of approximately 6,000 specimens has shown such a condition.

The above descriptions have referred to conditions of the mandibular cheek teeth. At each of the age intervals younger than 24 months the condition of the maxillary cheek teeth was checked. Variations in the time between the eruption, replacement or full development of the maxillary teeth as compared to opposing mandibular teeth were very slight. In general, coincident development was found in opposing teeth, but where variations did occur in individuals, the maxillary teeth were a bit slower in erupting.

PROCEDURE FOR DETERMINING AGE OF DEER

In determining the age of a white-tailed deer with the criteria given in this paper, the mandibular teeth are necessary. The first step is to determine the dental formula of the specimen in hand. This formula is the criterion necessary for aging the specimen according to one of the following six age classes:

		CLASS
At Birth to One Week	i. $\frac{0-0}{4-4}$; c. $\frac{0-0}{0-0}$; p.m. $\frac{0-0}{0-0}$; m. $\frac{0-0}{0-0}$.	1
One Week to Four Weeks	i. $\frac{0-0}{4-4}$; c. $\frac{0-0}{0-0}$; p.m. $\frac{2-2}{2-2}$; m. $\frac{0-0}{0-0}$.	2
Four Weeks to Ten Weeks	i. $\frac{0-0}{4-4}$; c. $\frac{0-0}{0-0}$; p.m. $\frac{3-3}{3-3}$; m. $\frac{0-0}{0-0}$.	3
Ten Weeks to Seven Months	i. $\frac{0-0}{4-4}$; c. $\frac{0-0}{0-0}$; p.m. $\frac{3-3}{3-3}$; m. $\frac{1-1}{1-1}$.	4
Seven Months to Thirteen Months	i. $\frac{0-0}{4-4}$; c. $\frac{0-0}{0-0}$; p.m. $\frac{3-3}{3-3}$; m. $\frac{2-2}{2-2}$.	5
Thirteen to Twenty-four Months and older	i. $\frac{0-0}{4-4}$; c. $\frac{0-0}{0-0}$; p.m. $\frac{3-3}{3-3}$; m. $\frac{3-3}{3-3}$.	6

The second step is further to subdivide these age classes into sub-classes or year classes. The first five age classes are broken into 11 sub-classes by criteria based on the eruption and loss of deciduous teeth and the stage of growth of the permanent dentition. The sixth age class is broken into three sub-classes from 13 to 24 months and eight sub-classes from $2\frac{1}{2}$ to $10\frac{1}{2}$ years of age.

CLASS 1. AT BIRTH TO ONE WEEK

Sub-class—At Birth. All incisors had erupted through the gum and approximately two millimeters of tooth showed through the gum. The premolars, although through the jaw bone, had not broken through the gum (Table 1).

The eruption of the incisors through the gum was checked on numerous embryos and apparently takes place two to three weeks before birth.

CLASS 2. ONE WEEK TO FOUR WEEKS

Sub-class—One to Two Weeks. The incisors showed further growth, the pincers measuring about three millimeters above the gum line on the labial side. At 10 days the incisors were almost fully erupted, measuring about four millimeters and at two weeks a fawn has a fully erupted set of temporary incisor teeth (Plate 4, *A*).

The premolar eruption started with the second and third teeth which were through the gum at one week. The first premolar may break through the gum at 10 days. However, this would only occur in precocious individuals.

Sub-class—Two to Four Weeks. The tooth formula at this period was not definite because the eruption of the first premolar was irregular (Table 1). The second premolar showed about one to two millimeters of tooth through the gum on the lingual side and the third premolar showed about two to four millimeters of tooth on the lingual side.

CLASS 3. FOUR WEEKS TO TEN WEEKS

Sub-class—Four to Seven Weeks. The premolars had erupted through the gum (Plate 4, *B*). The mesio-lingual cusp of the third premolar showed five to seven millimeters of tooth through the gum and the shoulder of all premolars (at the neck of the tooth) had not appeared through the gum. They were about half developed (Table 1).

Sub-class—Seven to Ten Weeks. On the third premolar about six to seven

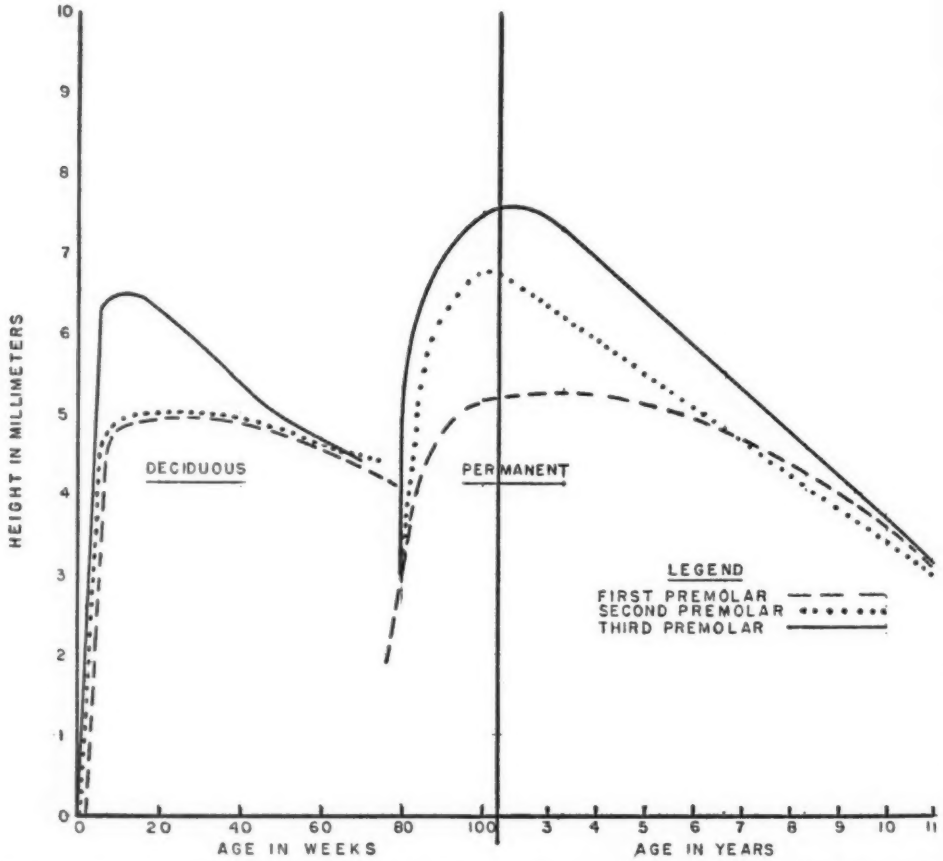

FIG. 2.—Development and decline of deciduous and permanent premolars of white-tailed deer showing height of lingual crest above the gum at various ages.

millimeters of tooth showed on the lingual side of the middle cusp. Also the small tubercles between the cusps of the third premolars on the buccal side appeared through the gum (note tubercles below gum line on 40-day specimen, Plate 4, *B*). At this stage the premolars were about three-quarters developed (Table 1). The shoulder on the first and second premolars was flush with the gum line and also flush with the shoulder of the anterior cusp of the third premolar. The shoulder on the second and third cusps was still covered by the gum (note location of shoulder on the 4-month specimen).

In addition to the above, the anterior cusp of the first molar came through the jaw bone at the eighth week and the second cusp of this molar can generally be seen through an opening in the jaw bone on defleshed jaws. Neither of these cusps pressed against the gum sufficiently to be felt in a live specimen nor could they be seen in a dead animal until the gum was removed.

Slight wear showed on the second premolar and on the anterior cusp of

the third premolar. No wear appeared on the first premolar or on the middle and posterior points of the third premolar.

CLASS 4. TEN WEEKS TO SEVEN MONTHS

Sub-class—Ten Weeks to Four Months. The gum line was flush with the shoulder on all three cusps of the third premolar. The anterior cusp of the first molar was through the gum line about two to four millimeters on the lingual side and about two to three millimeters on the buccal side (see Table 1 for age variations in the eruption of the first molar). The posterior cusps of the first molar broke through the gum one to two millimeters during the third month (Table 3). A hole in the jaw bone has started to form where the second molar would eventually erupt (Plate 4, *C*, 3-month specimen).

A little wear showed on the first premolar, moderate wear showed on the second premolar and the three cusps of the third premolar.

Sub-class—Four to Six Months. The only advancement in tooth develop-

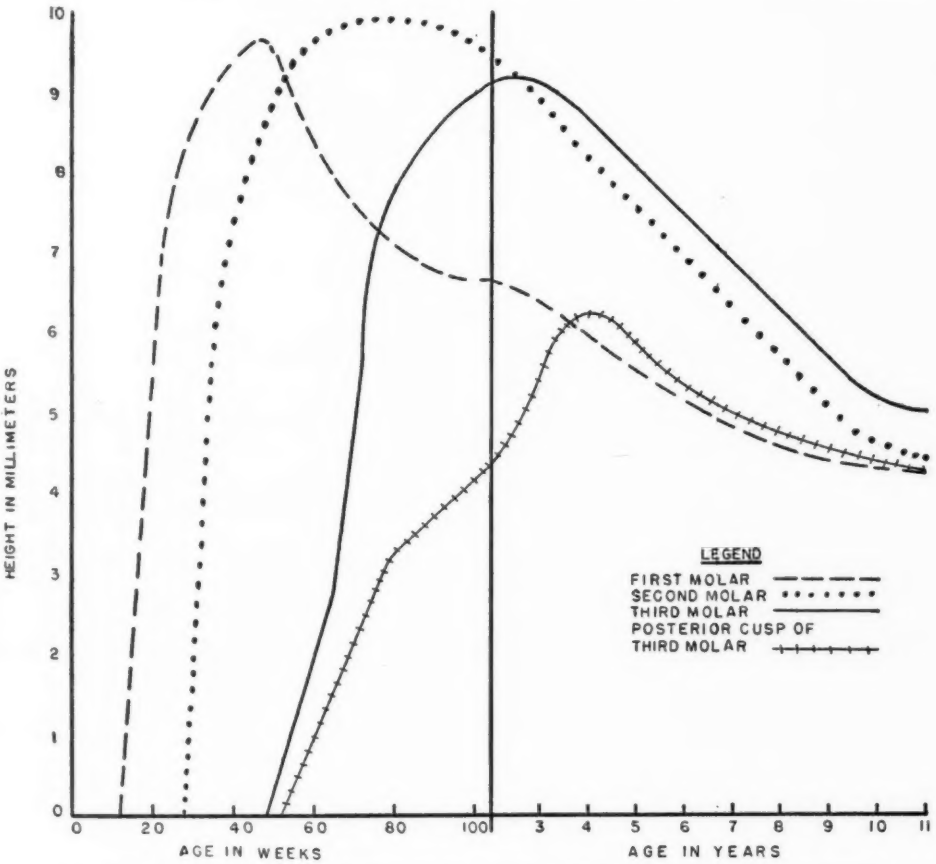

FIG. 3.—Development and decline of molars of white-tailed deer showing height of lingual crest above the gum at various ages.

ment was the further eruption of the posterior cusp of the first molar. It was through the gum about six to eight millimeters on the lingual side and about five to seven millimeters on the buccal side. The anterior cusp was through the gum about eight millimeters on the lingual side and six millimeters on the buccal side (Plate 4, *D*, 4-month specimen). The pincers were lost between the fifth and sixth months and replaced with permanent adult teeth although the latter were not fully erupted until the end of the sixth month. The replacement of these pincers was very rapid and necessarily so because fawns cut most of their food supply with these teeth.

Wear on the occlusal surfaces of the first temporary premolar was slight. Wear on the second and third temporary premolars was greater than that described in the previous period. However, no wear showed on the anterior cusp of the first molar.

Sub-class—Six to Seven Months. The adult pincers were fully erupted. Wear was slight on the first temporary premolar and conspicuous on the second and third. Slight wear showed on both cusps of the first permanent molar.

A variation in the time of eruption of the first molar was found. Seven of the specimens had four points erupted (Plate 4, *E*) while three specimens had only the two anterior points through the gum (Table 1). The second molar could be seen in one specimen (No. 277). In deer showing four points on the first molar, the anterior cusp of the second molar could be felt by pressing the gum. In all cases where the second molar had not erupted through the gum a hole in the jaw had formed through which the molar would erupt.

CLASS 5. SEVEN MONTHS TO THIRTEEN MONTHS

Sub-class—Seven to Nine Months. The second molar started to erupt during this period. Wear was moderate on the first temporary premolar and heavier on the second and third temporary premolars. Moderate wear showed on the first molar, slight wear showed on the anterior cusp of the second molar in specimen No. 225 but did not show on the second molar of the other six specimens. In these only one or two points of the second molar had erupted.

In the nine specimens examined, two (Nos. 173 and 174) showed only two points of the first molar through the gum (Table 1). However, these two specimens had grown slower than the others as judged by our records of weight and body measurements of deer of similar age. The first had not adjusted to captivity, and the second had been thyroidectomized on May 29, 1944. In the other seven specimens, three showed one point (anterior lingual), three showed two points and one showed three points through the gum on the second molar (Plate 5, *A*, 7-month specimen).

Sub-class—Nine to Eleven Months. During this period, replacement of the lateral incisors started, and the second molar continued its development. In all 15 specimens, wear was moderate on the first premolar and moderate to heavy on the second and third premolars. Slight to moderate wear showed on the first molar in all specimens showing four points of the second molar.

Wear on the anterior points of the second molar was slight on all specimens showing four points on this tooth but no wear showed on the second molar of those specimens in which only the anterior points had erupted.

During the ninth month, seven showed no change in incisor replacement from the foregoing period. Of these four showed two points (anterior) and three showed four points of the second molar through the gum. Of those showing four points, measurements of the posterior lingual cusps were four, five and five millimeters of tooth showing through the gum, respectively. On the other three specimens, all had lost the first lateral incisor, and in specimen No. 223 the right adult lateral incisor had fully erupted. In specimens No. 223 and No. 295 one or both of the second lateral incisors had been lost but not replaced (Plate 5, *B*, 9½-month specimen). The temporary corner incisors were all in place in the 10 specimens. In respect to the eruption of the second molar in these last three specimens, one had two points and two had four points showing (Table 1) on which five and six millimeters, respectively, of tooth showed through the gum line on the posterior lingual cusp.

During the ninth month one other change in tooth classification was made. In five specimens (Nos. 278, 219, 205, 299 and 295) the first molar was classed as adult. This molar (Table 1) was not classed as fully erupted until the second molar showed four points erupting through the gum.

During the tenth month five specimens were examined. Two (Nos. 172 and 173) showed normal tooth development. The former had replaced its lateral incisors with permanent teeth and the latter had replaced the first lateral incisor and had lost the second lateral and corner milk incisors on the left side. The first molar had fully erupted and four points of the second molar had erupted with the posterior lingual cusp showing six millimeters of tooth through the gum.

Tooth development was retarded in No. 174, a thyroidectomized deer, which was also underweight and small of stature. No change in tooth development occurred in No. 202 from the seventh to the tenth months. Those two deer lost five and three pounds, respectively, during the 3-month period.

Sub-class—Eleven to Thirteen Months. The replacement of all milk incisors with permanent teeth was completed and the second molar was fully erupted during this period. Wear on the premolars was not sufficiently different from that described at nine to 11 months to be designated. Also wear on the first and second molars did not change the appearance of the tooth.

In the five specimens examined, all showed normal tooth development. One specimen at 11 months showed all four points of the second molar and one point of the third molar. Two specimens showed four points on the second molar with nine millimeters of tooth on the posterior lingual cusp showing through the gum (Plate 5, *C*, 11-month specimen). Two, 12-month specimens, showed four points on the second molar with 10 millimeters of tooth showing on the posterior lingual cusp.

On the three 11-month specimens and the two 12-month specimens, a condition of the jaw around the roots

of the premolars had developed which could only be seen in a tissue-free jaw. Resorption of bone had started on the lingual side of the jaw beneath the three deciduous premolars. The permanent premolars were fully formed at this time and could be seen through a small orifice between the roots of each of the deciduous premolars in some specimens.

CLASS 6. THIRTEEN MONTHS TO TWENTY FOUR MONTHS AND OLDER

Sub-class—Thirteen to Seventeen Months. The third molar, erupting as the jaw elongated, came through the gum. Wear was moderate to heavy on the deciduous premolars and moderate on the first and second molars. No wear showed on any points of the third molar even in the September specimens.

Resorption of the jaw around the roots of the temporary premolars progressed. The permanent premolars continued to push up closer to the base of their deciduous precursors.

In the one specimen examined (No. 295), the deciduous premolars were held fast by their roots, and two anterior points of the third molar erupted (Table 1) with three millimeters of the anterior lingual point showing through the gum.

Further confirmation of the development of the third molar was gained through an examination of eight deer killed in the wild during the months of July, August and September. These deer were 13, 14, and 15 months old, respectively, assuming an average fawning date of June 1 (Cheatum and Morton, 1946). Three July specimens showed both points of the anterior cusp of the third molar; three August specimens showed both points of the anterior cusp and the lingual point of the median cusp; two September specimens showed the above mentioned points

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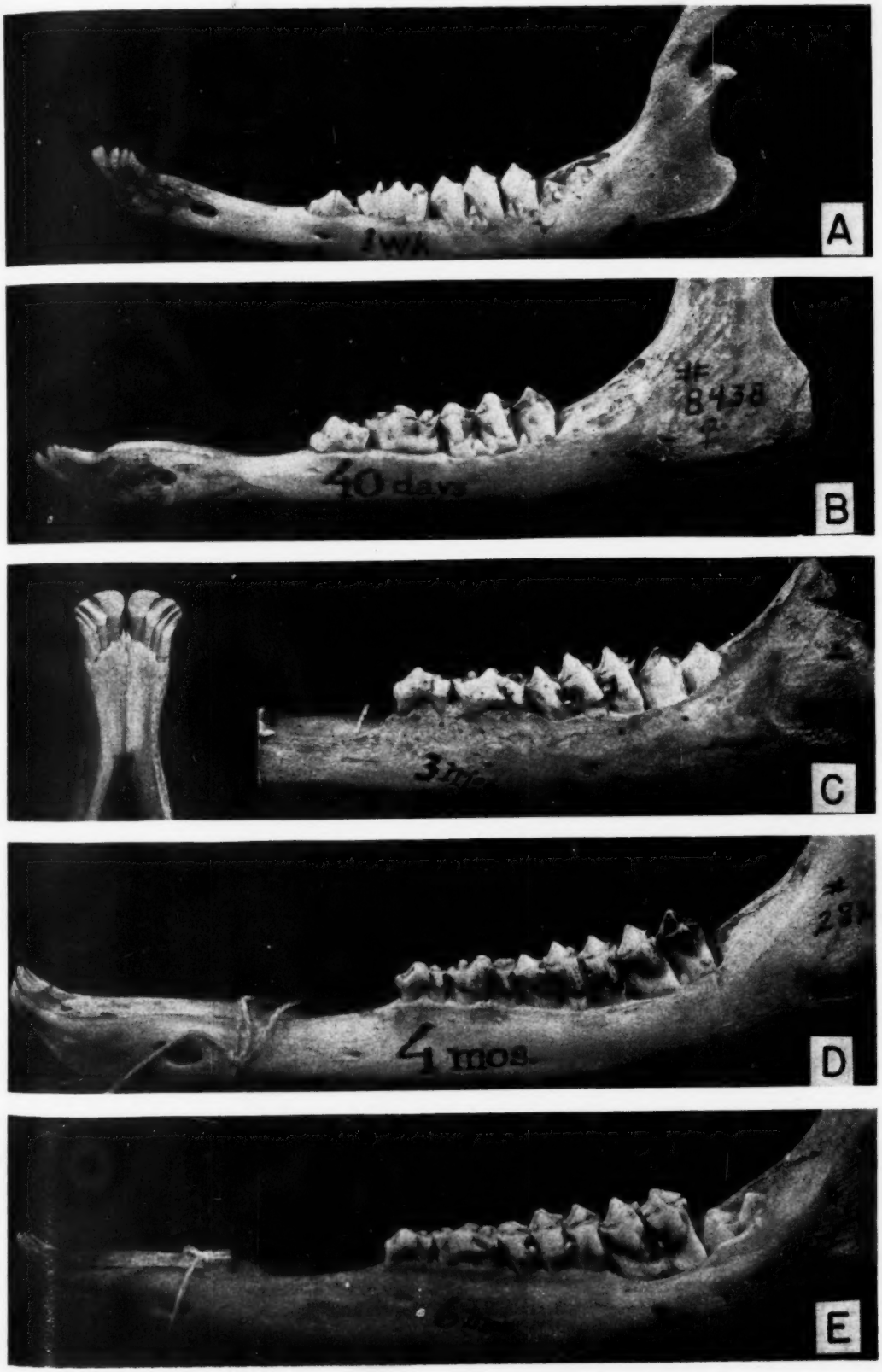
EXPLANATION OF PLATES 4–7

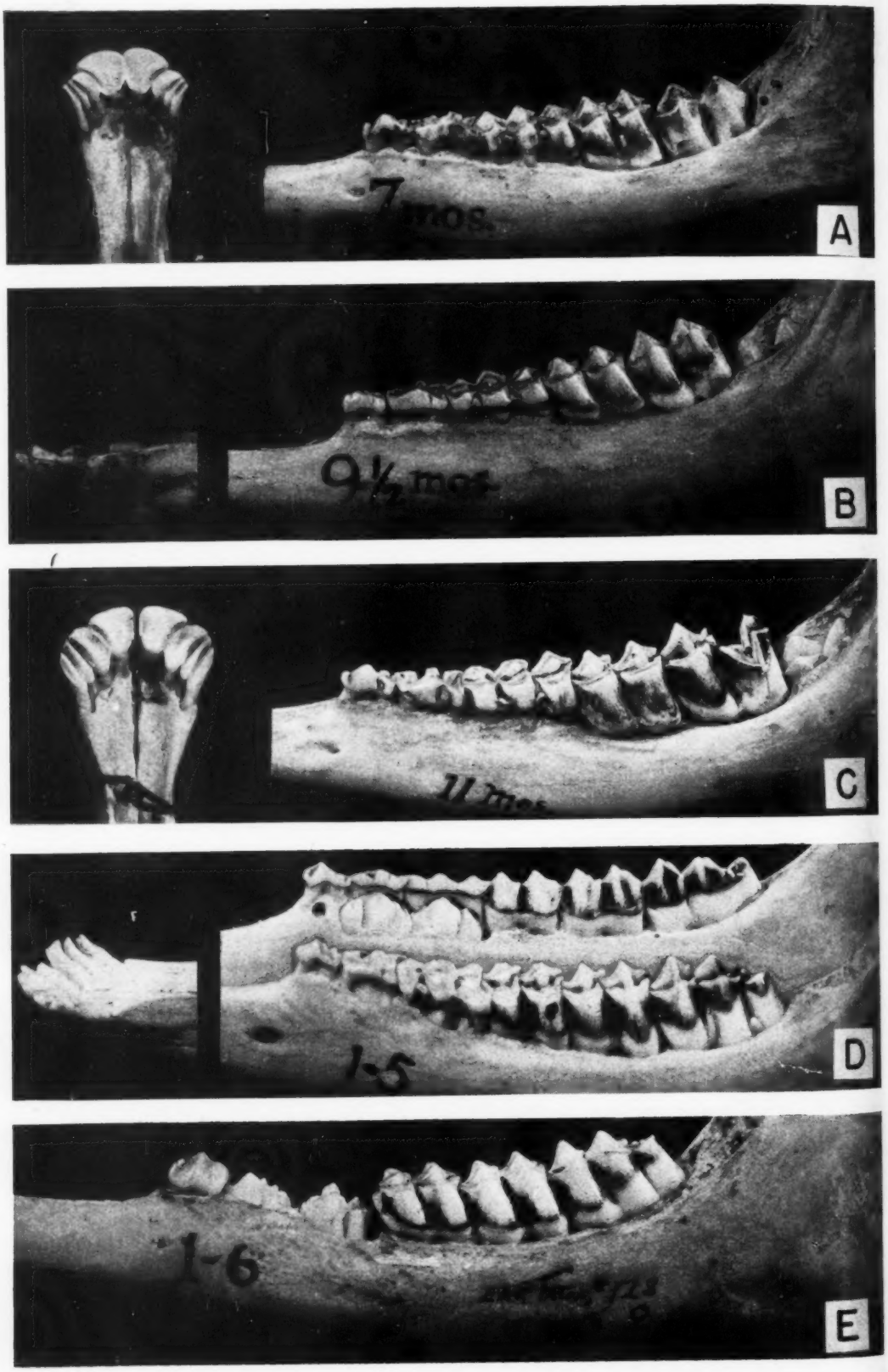
PLATE 4.—Condition of teeth of white-tailed deer at: *A*, one week; *B*, forty days (note appearance of tartar line); *C*, three months (note small milk incisors and three cusps of third milk premolar); *D*, four months; *E*, six months (incisors lost, but normally all would be present). Natural size.

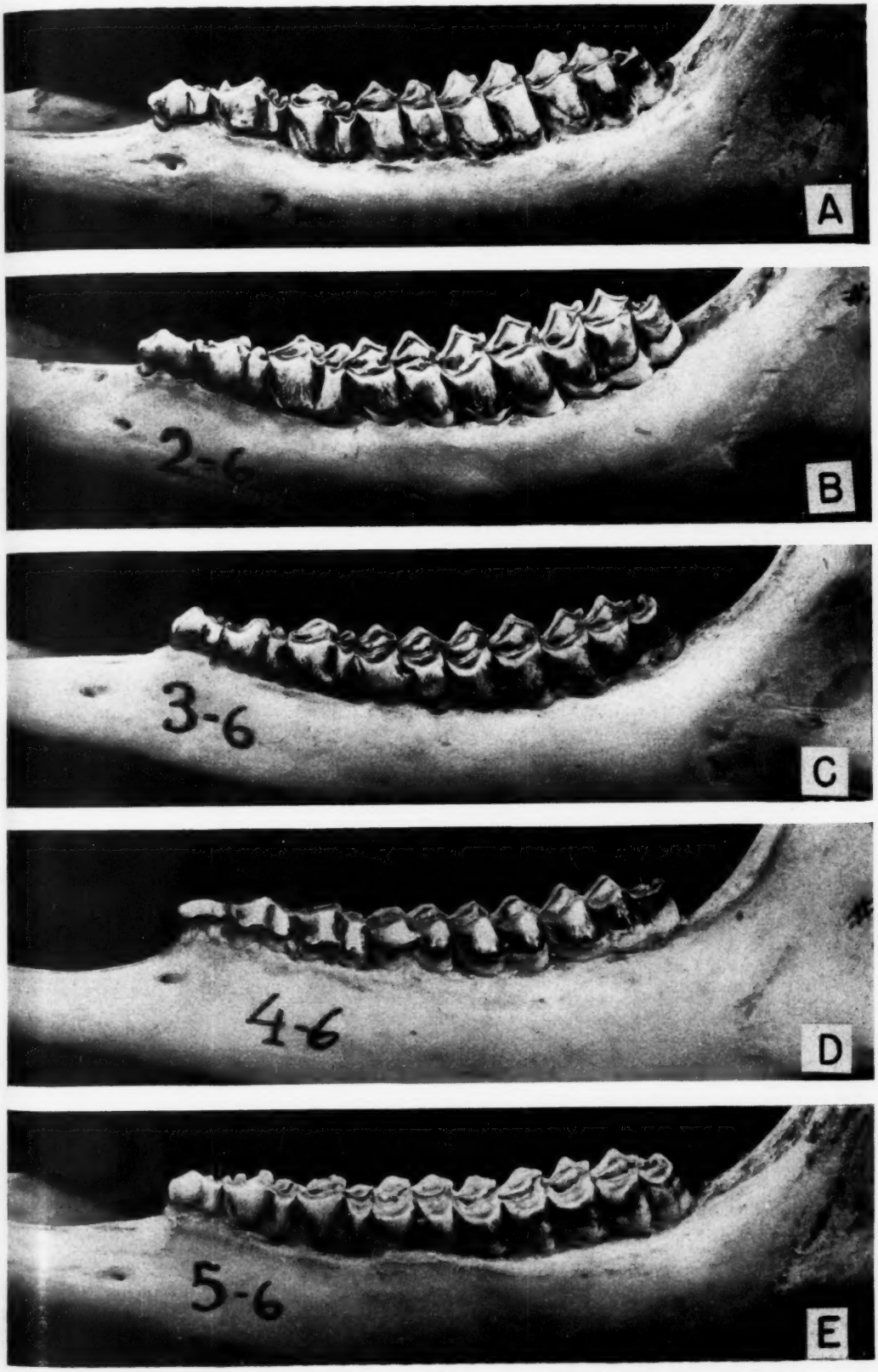
PLATE 5.—Condition of teeth of white-tailed deer at: *A*, seven months (note presence of adult pincers); *B*, nine and a half months; *C*, eleven months (note presence of adult lateral and corner incisors); *D*, one year and five months, showing exterior aspect of left lower jaw as in other specimens pictured and interior aspect of right lower jaw (note heavy wear on all milk premolars and, in interior view, appearance through jaw bone, but not gum, of permanent premolars); *E*, one year and six months (note loss of milk premolars and appearance through gum of permanent premolars). Natural size.

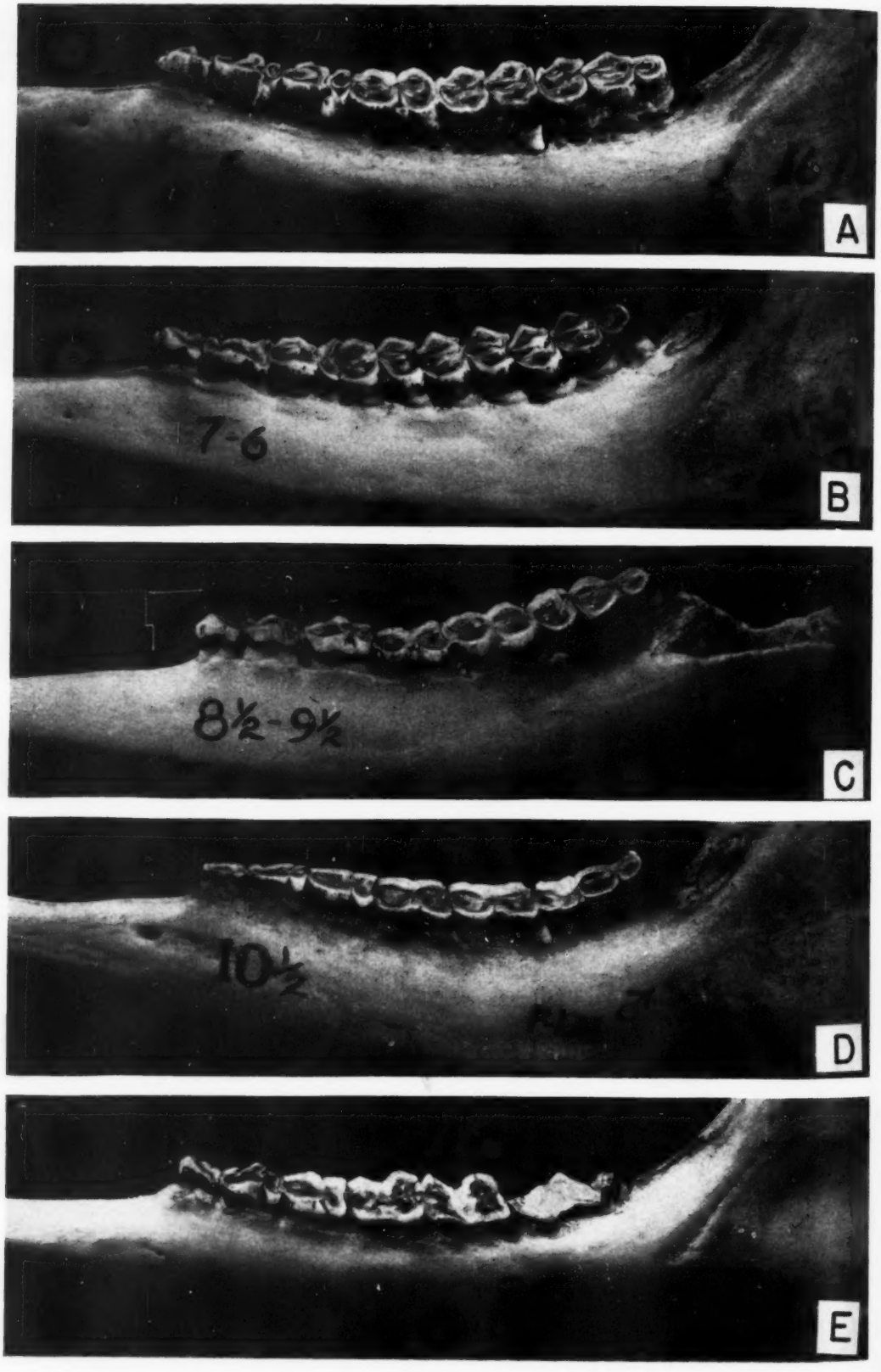
PLATE 6.—Condition of teeth of white-tailed deer at: *A*, two years (note sharp ridges of all molars and very slight wear on posterior cusp of third molar); *B*, two and a half years; *C*, three and a half years (note further wear on all molars, especially first molar); *D*, four and a half years (note lingual crests of first molar are worn away and further wear on all molars); *E*, five and a half years (note lingual crests of first and second molars are worn away and further wear on third molar). Natural size.

PLATE 7.—Condition of teeth of white-tailed deer at: *A*, six and a half years (note absence of lingual crests on all molars); *B*, seven and a half years (note additional wear on molars and heavy wear on premolars); *C*, eight and a half years to nine and a half years; *D*, ten and a half years (all teeth worn close to gum line); *E*, old age (probably about 12 years; teeth worn until pulp cavity is exposed). Natural size.


1 wk
A
#8438
40 days
B
3 mos.
C
4 mos.
D
E


7 mos.
A
9½ mos
B
11 mos
C
1-5
D
1-6
E


A
2-6
B
3-6
C
4-6
D
5-6
E


A
7-6
B
8½-9½
C
10½
D
E

and the buccal point of the median cusp.

Sub-class—Seventeen to Twenty Months. The temporary premolars had been replaced by adult teeth during this period and the permanent premolars had erupted sufficiently during the last month of the period so that wear had begun to show on the occlusal surfaces of these teeth. All points of the third molar erupted, although not fully.

Of the eight specimens examined, one (18 months old) still held the second and third premolars in place on the left side. The first permanent premolars were fully erupted, the second and third premolars on the right side were lost and all points of the third molars erupted. Five specimens 18½ months old were examined. The temporary premolars were in place on two of these (Nos. 152 and 127) as shown by the 1-year and 5-month specimen in Plate 5, *D*. On one (No. 127), all cusps of the third molar were through the gum and on the other (No. 152) the anterior and median cusps were through the gum. On the other three specimens (Nos. 138, 139, and 145), the temporary premolars had been shed (Plate 5, *E*, 1½-year specimen). The permanent premolars were about three-quarters erupted except for the first premolar (right jaw) of one specimen which was just protruding through the gum. The third molars of these three specimens showed all cusps through the gum. Two specimens 19 months old (Nos. 5 and 129) were examined. The former had all of the permanent premolars fully erupted and all cusps of the third molar were through the gum. The latter had been on an inadequate browse diet during the last two months of its life, and in it, the temporary premolars were still rigidly in place and the succedaneous teeth had barely pushed through the jaw bone. All cusps of the third molar were through the gum and in a normal position in both of these specimens.

Because of the variation in replacement of the premolars, wear on the teeth must be described by grouping the jaws. One specimen (No. 128) showed no wear on the permanent premolars, moderate wear on the first and second molars and slight wear on all cusps on the third molar. Two specimens (Nos. 127 and 162), still holding temporary premolars, showed heavy wear on the temporary teeth with the lingual side averaging two millimeters in thickness from the gum to the occlusal surface. Wear on the first and second molars in these two specimens was moderate and showed slightly on the anterior cusp of the third molar. Three specimens (Nos. 138, 139 and 145) had lost the temporary premolars, and no wear showed on the adult teeth. Moderate wear showed on the first and second molars, and wear on the third molar was slight on the anterior and median cusps. Two specimens (Nos. 5 and 129) showed a great variation in tooth replacement. Specimen No. 129 showed wear condition typical of that described above for Nos. 127 and 152 in which the temporary premolars were still in place. Specimen No. 5, believed to be more typical of deer one year and seven months of age, showed slight wear on the permanent premolars, while wear on all molars was typical of that described for specimens No. 138, 139 and 145.

Sub-class—Twenty to Twenty-four Months. During this period, the third molar erupted fully to complete the

development of adult dentition. The two specimens examined were one year and 11 months of age. All teeth were fully erupted, and the occlusal surfaces of the mandibulary and maxillary teeth met. Full eruption was probably completed by the 21st month judging from the wear on the teeth (Plate 6, *A*).

Wear was slight on the premolars, moderate on the first and second molars and light on the third molar.

Sub-class—Two and a Half Years. The primary criteria for this class were the condition of the first molar and the posterior cusp of the third molar. The lingual crests of the first molar were sharp with the enamel well above the narrow dentine of the crest. Wear on the posterior cusp of the third molar was slight, and as the elongation of the jaw was not complete, the gum line around this cusp had not retracted sufficiently to expose the full height of this cusp.

Secondarily, there was generally very little wear on the first premolar, slight wear on the second and third premolars. The lingual crests of the second and third molars were sharp with the enamel well above the dentine. Slight buccal crests were present on these molars and stood out slightly above the dentine of the cusp. The dentine of the buccal crests was of moderate width and presented a slight cusp edged with enamel.

The sides of the infundibulum of the third premolar and of all the molar teeth formed a broad conspicuous V. When viewed from above, the infundibular opening formed a crescent design in the occlusal surface of the teeth (Plate 6, *B*).

Sub-class—Three and a Half Years. The primary criteria for this class were the condition of the first molar and the posterior cusp of the third molar. The lingual crests of the first molar were blunt and the dentine of these crests was wider than the enamel. The posterior cusp of the third molar was flattened by wear forming a definite concavity in the occlusal surface.

Secondarily, there was little wear on the first premolar, slight wear on the second premolar, moderate wear on the third premolar and the lingual crests of the second and third molars formed a narrow line about the width of the enamel. The buccal crests of the molars sloped laterally downward and the dentine in the crests of the first and second molars was wider than the enamel (Plate 6, *C*).

The sides of the infundibulum of the third premolar, and of the second and third molars formed a broad conspicuous V. The first molar was worn sufficiently to reduce the infundibulum to a shallow horizontal crescent.

Sub-class—Four and a Half Years. The primary criteria for this class was the condition of the first molar and the posterior cusp of the third molar. The lingual crests of the first molar were almost worn away, and the dentine of these crests was almost twice as wide as the enamel (Plate 6, *D*). The posterior cusp of the third molar was worn at the edge of the cup so that the occlusal surface sloped laterally downward.

Secondarily, there was little wear on the first premolar, moderate wear on the second, and moderate to heavy wear on the third premolar so that much of the crest was worn away on this latter tooth. The lingual crests of the first molar were almost worn away. The lingual crests of the second molar

were about as dull as those on the first molar in a 3½-year specimen. The same cusps on the third molar were worn similarly to those of the first molar in a 2½-year specimen. The dentine of the lingual crests of the second molar was wider than the enamel while on the third molar it was about as wide as the enamel. The dentine of the buccal crests of the first and second molars was much wider than the enamel, and the laterally downward slope was maintained.

The infundibulum of the third premolar and of the second and third molars was reduced to a shallow, narrow groove. In the first molar it was only a fine crescent or chevron-shaped design on the occlusal surface of the tooth. In some places in the first molar of various specimens it was worn away.

Sub-class—Five and a Half Years. The primary criteria for this class were the condition of the first and second molar. No lingual crests were left. If an imaginary line were drawn from the lingual to buccal edges of these teeth it would generally touch the enamel on either side of the infundibulum. The occlusal surfaces of these teeth were sloped laterally downward starting on the lingual side and extending across the flattened tooth. Because of the slope of the occlusal surface, the horizontally rounded lingual edges of the first molar appeared like crests but the original crests were worn away (Plate 6, *E*).

Secondarily, the first premolar was slightly worn, and moderate to heavy wear showed on the second and third premolars. The lingual crests of the third molar were blunt, like those of the first molar of a 3½-year specimen. The dentine of the lingual crests of all molars was broader than the enamel, and a similar condition existed with the dentine in the buccal cusps.

The infundibulum appeared as a fine crescent or chevron-shaped design on the first molar and had disappeared in some places. On the third premolar and on the second and third molars, the infundibulum appeared as a narrow, crescent-shaped design on the occlusal surfaces of these teeth.

Sub-class—Six and a Half Years. The primary criteria of this class were the condition of the molars and premolars. There were no lingual crests on the first molar, almost no lingual crests on the second molar, and a slight lingual crest on the third molar. Wear was moderate on the first premolar and heavy on the second and third premolars. The premolars, therefore, showed wear at this stage. This condition, appearing for the first time on the fully erupted permanent premolars, might cause some confusion with the heavily worn temporary premolars of a deer from one year and four months old to one year and six months old previously described. The three-cusped third premolar of the temporary teeth as compared to the two-cusped tooth of the permanent teeth will easily separate the two classes (Plates 5, *D* and 7, *A*).

The infundibulum appeared as a fine line or chevron design on the first molar and was absent in some places. On the third premolar the infundibulum appeared as a small triangular hole, and in the second and third molars it was a narrow, crescent design showing only a slight depth.

Sub-class—Seven and a Half Years. The primary criteria of this class were

the condition of the molars and premolars. The first molar was worn down within two or three millimeters of the gum line on the buccal side and four to five millimeters on the lingual side. The second molar was almost smooth, and the third molar had worn down until the lingual crests were completely gone. The premolars showed heavy wear and were much flattened (Plate 7, *B*).

The infundibulum was almost gone from the third premolar. It was worn out of the first molar, sometimes remained in the second as a fine line or chevron design, and was present in the third molar as a narrow, crescent-shaped line which still showed some depth.

Sub-class—Eight and a Half and Nine and a Half Years. In this class wear on all premolars and molars had reduced the entire set of mandibular cheek teeth to about two to three millimeters of tooth above the gum on the buccal side and four to five millimeters on the lingual side. The infundibulum had worn away on the third premolar and on all molar teeth. In the cusps of all cheek teeth the dentine was joined (Plate 7, *C*).

Sub-class—Ten and a Half Years and Older. Wear on all mandibular cheek teeth of deer in this class continued beyond that described for the preceding class. The premolars and molars were worn to the gum line or within two millimeters of the gum on the buccal side and two to five millimeters on the lingual side. In the cusps of all cheek teeth the dentine was joined. In some specimens the dentine of these teeth was completely worn away exposing the pulp cavity (Plate 7, *D*).

At this age some specimens had lost the pincers and sometimes the lateral incisors. One or both of the pincers were occasionally missing among younger deer from seven and a half years and up. In addition, 60 specimens from the wild had shown that the loss of adult incisors is not a constant character of age for any of the older age classes.

Old Age. Recognition of a ten and a half year sub-class should not be construed as an indication that it is the maximum age of a deer. Major Flower (1931) described the life duration of the family Cervidae as follows: "The medium and large-sized species of Deer have specific longevities of from eight to twelve years, and potential longevities up to twenty-three years. Males and females appear to have lives of about equal length. Taking two hundred representative individuals of both sexes, I find that the hundred males average ten years, four months, nine days and the hundred females ten years, ten months, twenty-seven days." In addition, Major Flower stated that "Twenty individual American Deer of the genus *Odocoileus* average a life of eight years, ten months, six days. The longest records for Mule Deer, *Odocoileus hemionus* in London Z. G. are of a female . . . 11 years 4 months 17 days, and of a male . . . 12 years 2 months 15 days. A male peruvian Deer, *Odocoileus peruvianus*, which was presented to the London Z. G. . . . lived there till . . . its age was at least 13 years 1 month. R. L. Ditmars (1919) has recorded a 'Florida Deer' as living for 15 years in the New York Zoological Society's Park." Cowan (1936) reported measurements of antler developments throughout life by a male coast deer (*O. h. columbianus*) and this deer apparently reached an age of at least 16

years. A record was reported to the author by Ranger Walters of Allegany State Park in the fall of 1945. This female was still alive at the time and would be 16 years old in the spring of 1946. This deer had had access to vegetables, apples, hay, grain and the shelter of a barn during the winter season, but it was more or less free to wander except during the hunting season. Osgood (1922) stated "the normal life of these deer [white-tails] is seldom over ten years" and Huxley (1931) recorded the "highest age" of red deer from records at Warnham Park as "14 years."

These records indicated that individual deer could live to be 14 to 16 years of age, possibly older. Nevertheless, all of these deer of extreme old age had either been held in captivity where foods other than their normal browse diet were provided or they were provided with foods which were softer and possibly more nutritious. On the other hand, most of the deer used in this study as the basis for the age classes above two years of age fed on a normal browse diet. These deer, seven, eight, nine and ten years old, were wearing or had worn their teeth down close to the gum. The teeth in the 10-year specimens were almost worn down to the gum. Therefore, above this age the smooth condition of the teeth, the possibility of exposure of the pulp cavity, and gum infections may become a limiting factor of maximum life expectancy of wild deer.

DISCUSSION

The appearance, development and subsequent wear of the teeth is recognized as a dependable means of judging the age of domestic animals. This paper described these same characters of dentition in wild white-tailed deer. In marked contrast with most domestic animals which acquire their permanent dentition at ages from four to seven years, a deer attains its permanent dentition before it is two years old. During this rapid development of the adult dentition, fourteen age classes are recognized.

Other authors (Cahalane, 1932; McLean, 1936; Cowan, 1936; Park and Day, 1942) have described the development of the adult dentition of North American deer. Their descriptions, in each case, are based on a small number of known-age specimens and as a consequence specific developments in dentition are described as occurring within broad age classes. The tooth developments described by these authors for the various ages approximated the age at which similar developments occurred during the present study. In order to point out differences which did occur in the studies of the above mentioned authors the stages of development and the associated ages as described by the various authors are summarized in Table 3.

Rörig (1915) published some data on the tooth development in European Deer. He gave the age at which the premolars and molars came into use in three European deer as follows:

	Red Deer	*Fallow Deer*	*Roe Deer*
Set of milk teeth	First 6 months	First 6 months	3½ months
First molar	7 to 18 months	7 to 15 months	Middle of 4 to 7 months
Second molar	19 to 30 months	16 to 24 months	8 to 13 months
Exchange milk for permanent premolars	Middle of 3rd to end of 4th year	End of 2nd to 4th year	14 to 30 months

TABLE 3.—SUMMARY OF TOOTH DEVELOPMENT AND REPLACEMENT AT CERTAIN AGES IN DEER OF THE GENUS ODOCOILEUS AS DESCRIBED BY VARIOUS AUTHORS

Tooth development and replacement	Authors[d]				
	Present author	Cowan[a]	McLean[a]	Cahalane[b]	Park[b]
Milk incisors present	At birth, 2mm. above gum	Before birth	At birth		
Incisors fully erupted	10 days to 2 weeks				
2nd and 3rd premolar erupted	During 1st week	Before or at birth			
1st premolar erupted	10 days to 4 weeks				
1st, 2nd and 3rd premolars fully erupted	By the 10th week	By 2 months	At birth		
1st molar erupted	During 3rd and 4th months	By 3½ months[c]	At birth		
1st milk incisors (pincers) lost	During 5th month				
1st adult incisors (pincers) fully erupted	During latter half of 5th month and during 6th month	At 1st year	10 to 12 months	Acquiring at 9th month	By 9th month
2nd molar erupted	During 7th and 8th months	At 1st year		Acquiring at 9th month	By 9th month
1st molar fully erupted	During 7th month		5 to 6 months	Acquiring at 9th month	By 9th month
1st and 2nd lateral milk incisors lost	During 9th and 10th months	By 14 months		Still milk at 9 months	
Corner milk incisor lost	During 9th and 10th months				
1st and 2nd lateral incisors fully erupted	During 10th and 11th months	By 14 months	10 to 12 months	By 18 months	By 18 to 21 months
Incisor corners fully erupted	During 10th and 11th months	By 18 months	10 to 12 months	By 18 months	By 18 to 21 months
2nd molar fully erupted	During 12th and 13th months	By 15 to 18 months		By 18 months	By 18 to 21 months
3rd molar erupted	During 11th and 12th months	By 15 to 18 months	In second year	By 18 months	By 18 to 21 months
Milk premolars lost	During 17th and 18th months		In second year	Much worn by 18 months	
Adult premolars fully erupted	During 18th and 19th months	By 24 to 25 months	Latter part of second year		
3rd molar fully erupted	During 19th and 21st months	By 24 to 25 months	Latter part of second year	By 18 months in precocious individuals	
Complete permanent dentition	By end of 21st month		Latter part of second year		At about 30 months

[a] Refers mainly to *O. hemionus*

[b] Refers mainly to *O. virginianus*.

[c] Appearance of the 1st molar by 3½ months agrees well with the observations of the present author. Cowan, however, also used the expression "in functional tooth row" to describe the development of this tooth at this time which suggests a more advanced stage.

[d] The author regrets that the work of Gilbert N. Hunter, "Physical Characteristics of Colorado Mule Deer in Relation to their Age Class," (Game and Fish Dept. Denver, Colo.) was not available to him when this paper was written. Mr. Hunter's work states the tooth replacement of Colorado mule deer to be "exceedingly irregular" and completely different from that of the white-tail. It is also different from the replacement described by Cowan and McLean. Hunter says, "first permanent incisors are not cut until the deer is around one year old," . . . other incisors "may be cut between the ages of 12 and 16 months, . . . milk premolars are usually shed between the ages of 30 and 32 months," . . . and, "a deer has a full mouth when he is 3½ years old."

The ages at which these teeth came into use in the roe deer approximates the age of full eruption in the white-tail but in the other two species a great difference exists.

The condition of the teeth at various stages of development or wear are illustrated by Cahalane, and Park and Day. Some of these illustrations do not agree with the conditions found in the present study. The illustration by the former author "at about nine months of age" is typical of the condition found at six or seven months in this study. The illustration of the "nine-month age class" by Park and Day approximates the tooth condition found in this study at $1\frac{1}{2}$ years. The other illustrations appear to be within the age group designated except for the $5\frac{1}{2}$-year plus and $9\frac{1}{2}$-year plus classes of Park and Day. These appear very similar to the $4\frac{1}{2}$- and $7\frac{1}{2}$-year classes described in this study.

In addition to the differences pointed out above, Cowan, working with *O. h. columbianus*, stated that "at the age of 15 months the median root of the deciduous fourth premolar is being dissolved." In this study only three deciduous premolars were found. As for the dissolving of the roots of these deciduous premolars, they were found to begin dissolving at 11 months of age in this study.

Park and Day, working with *O. virginianus*, in their caption describing the molar teeth of the "nine-month-age class" stated "these molars [first and second] are all milk teeth and are much smaller than the permanent . . . molars . . . !" In the present study, these teeth described by Park and Day were found to be permanent adult molars and not milk teeth.

Canine teeth are also described as occurring in deer. Cahalane notes a "canine" in the maxillary tooth row of an illustration of the 9-month condition. Cowan, on the other hand, states that the fourth incisors (corners, Figure 1) of a deer are canine teeth and describes them as incisor-like canines. The occurrence of canine teeth in New York white-tails, except for the corners, was infrequent. To date over 6,000 deer have been examined and only five specimens have been found. In every case their occurrence was restricted to the maxillary row.

The pattern of tooth development described by Cowan and McLean in *O. hemionus* differs from that described by the present author. These differences were discussed with Cowan in February 1947 and afterwards he rechecked his series of data. This recheck was made with a group of specimens from Vancouver Island. In his letter (March 10, 1947) Cowan stated that the only "point of major disagreement" with his published data was "with regard to the replacement of the premolars which in the Vancouver Island material definitely starts later than it did in my series from California; about two months later on the average." Thus it would appear that there is not a uniform pattern (Table 3) of tooth development in the entire genus of *Odocoileus*. Similarly, Rorig's data indicates that the red deer (*Cervus elaphus*) and the fallow deer (*Cervus dama*) differ widely from species of *Odocoileus*. On the other hand, Rorig's data on the development of the teeth in the roe

deer (*Capreolus capreolus*) was very similar to that described for the white-tail (*Odocoileus virginianus*).

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AGING COTTONTAIL RABBITS BY BONE GROWTH

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A precise age criterion has long been needed for the cottontail rabbit (*Sylvilagus floridanus*). Few species have been as extensively studied, and no species yields so large a fraction of the total bag of game, yet we have been unable to tell what part of the cottontail bag is breeding stock (adult rabbits) and what part is young of the year. The only published age ratios I have discovered appear in annual reports of the Rose Lake, Michigan, Wildlife Experiment Station. These ratios were compiled each hunting season from trapped and shot cottontails, and are summarized in Table 1. Females were classified for age by the size and condition of teats; males by body size or from ear tags placed earlier in the summer.

Several age indicators have been developed, but none is valid through a hunting season. Dice and Dice (1941) aged young cottontails by the enamel pattern of molariform teeth. After a

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rabbit attains a full set of teeth at about one month of age this criterion is no longer of value. Beule and Studholme (1942; *in litt.*) aged juveniles by tarsal measurement until a length of 85 mm. was reached at about 16 weeks of age. The daily tarsal growth rate of all litters was two millimeters from a length at birth of 19 mm. Elder and Sowls (1942) were able to classify the age of cottontails by autopsy until December. They found that young males have turgid testes and old males have flaccid testes; adult females have placental scars in their uteri, but juvenile females do not. Placental scars may not always be accurate indicators of adult cottontails; Cooley (1936) and Hendrickson (1947) cite records of known-age juvenile females breeding in their first summer.

Weights and external measurements are not reliable for determining age in winter, because young cottontails grow very rapidly. Elder and Sowls (1942) found some juveniles weighed more than known adults as early as August. Allen (1939) says that young rabbits attain full growth by December.

TABLE 1.—MICHIGAN COTTONTAIL AGE RATIOS

Year	No. of Rabbits	No. of Young	No. of Old	Per cent of Young	Source
1940	140	79	61	*56*	Allen, 1941
1941	248 (females only)	172	76	*69*	Allen, 1947a
1942	619	400	219	*65*	Allen, 1947b
1943	268	160	108	*60*	Michigan, 1947a
1944	157	52	105	*33*	Michigan, 1947b
1945	126	75	51	*60*	Michigan, 1947c

THE BONE CRITERION OF AGE

The presence or absence of epiphyseal cartilage in long bones such as the tibia, humerus, and femur has been used for many years by medical science to age primates and laboratory animals, but the method has only recently been applied to a wild game species.

In newborn cottontails a thick plate of epiphyseal cartilage is found between the diaphysis, or shaft, and the epiphysis, or head, of long bones (Plate 8, *A*). The cartilage area is a growth center where proliferation of cartilage and its replacement by bony tissue results in elongation of the bone. As a rabbit grows older, the cartilage plate gradually decreases in thickness due to a regression of cell division (growth), and eventually is replaced entirely by bone during a rabbit's first winter. Bones of adult cottontails have no epiphyseal cartilage. In following discussions, the term "open epiphysis" means that epiphyseal cartilage is present and the term "closed epiphysis" that no cartilage is present.

Thomsen and Mortensen (1946) were the first to study cottontail bone growth as an age criterion. They found that young of the year could be differentiated from adults by the presence of epiphyseal cartilage. They did not establish the time limits within which the bone test was valid, nor did they verify it with tagged animals of known age. This paper attempts to do both.

The age at which epiphyseal cartilage

disappears in the earliest-born young is very important, because a population can be classified for age with accuracy as to individuals only up to the date on which epiphyses close in the earliest-born young. For example: If a cottontail born at the beginning of the breeding season in April had closed epiphyses on January 1, then any age ratios taken after January 1 would be inaccurate due to the probable presence of rabbits of the year with epiphyses already closed.

In this study a limiting date was determined from a series of cottontails of known age taken during fall and winter. The approximate age of these rabbits was known because they had been trapped as juveniles, marked, and released the previous summer.

The humerus, or upper bone of the foreleg, was selected for study, although epiphyseal cartilage seems to remain longer in the upper tibia than in the humerus. When large-scale bag examinations are made, hunters are more apt to give up a forelimb than other more meaty portions of a carcass.

METHODS OF OBTAINING RABBITS FOR STUDY

Live trapping of young cottontails during summer was very successful (Table 2). Treadle-type box traps of all-wood construction were used, and all trapping was done at the 1,000-acre University of Wisconsin Arboretum. One hundred thirty-three cottontails weighing up to 900 grams at first trapping were classed as young of the year without question. The age of 101 cottontails weighing more than 900 grams at the first trapping was estimated and later checked by the bone test when retaken in winter. A few of the latter tagged cottontails were recaptured too late in the winter to be satisfactorily classified for age.

Each cottontail was marked in two ways. A numbered metal tag was placed in one ear. The other ear was tattooed with a number applied by a commercial tattooing pliers. Both methods proved to be adequate markers, and tattoos seem to last indefinitely. Two cottontails captured 18 months after marking bore easily readable tattoos.

Tagged cottontails were moved from their trapping site, and all were liberated at the same point on another Arboretum area. This was done to make winter recapture easier. It also provided limited information on the dispersal of cottontails released on a strange range. Straight-line dispersal distances from the point of release varied from 50 feet to nearly a mile, averaging 1,100 feet. Correlations were not evident between dispersal distance and sex, age, date of release, date of recapture, release-recapture interval in days, or weight at release. Only one of 245 tagged cotton-

TABLE 2.—COTTONTAIL TRAPPING SUMMARY

	Summer 1945	Winter 1945–46	Summer 1946	Winter 1946–47	Total
Rabbits tagged & released	76		158		234
Tagged rabbits trapped		13		22	35
Untagged rabbits trapped		41		39	80
Trap nights/rabbit caught	36	14	40	34	

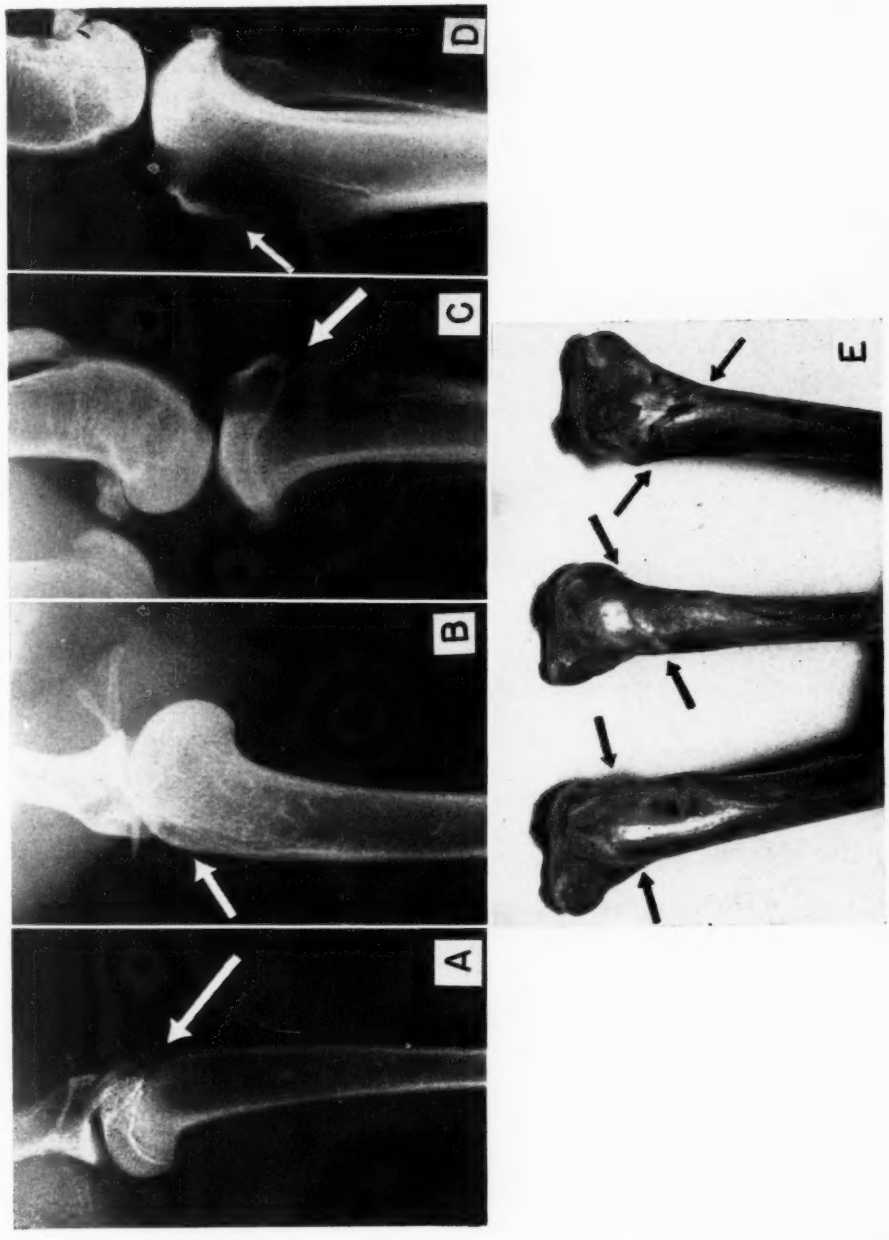

PLATE 8.—*A*, Humerus of young cottontail; epiphyseal cartilage plate present and indicated by notch and white line in the epiphyseal region (arrow). *B*, Adult humerus; epiphyseal cartilage plate has disappeared, and notch and line diagnostic of juvenile epiphysis absent. *C*, Young tibia; cartilage present, as shown by notch and line. *D*, Adult tibia; cartilage absent and notch has disappeared. *A* to *D*, X-rays. *E*, In humerus of a young cottontail (right); epiphysis open and external cartilage groove (arrows) wide and distinct. In humerus of nearly-mature cottontail (center), epiphysis is smaller, although still open, and cartilage groove is becoming indistinct. Humerus of adult (left) has a closed epiphysis, and no cartilage groove present.

tails liberated on the release area over a two-year period returned to the place where it was trapped. This animal moved the 4,950 feet between point of release and point of recapture in not more than seven months.

Marked cottontails were recaptured in fall and winter by trapping (Table 2) and by shooting from November 1 to April 1. The largest number of winter cottontails were taken by shooting. Rabbit hunts were held periodically throughout each winter, with 3 to 9 men participating in each shoot. Cottontails were less abundant during the second winter, as indicated both by bag and flushing rate (Table 3).

TABLE 3.—WINTER HUNTING SUMMARY

	1945–46	1946–47	Total
Number of hunts	10	29	39
Kill per gun-hour	1.2	0.5	
Rabbits flushed per hour	—	1.04	
No. of tagged rabbits shot	10*	19**	29
No. of untagged rabbits shot	204	152	356

* Includes one cottontail tagged in 1944.
** Includes two cottontails tagged in 1945.

The total number of winter cottontails taken by all methods for bone growth studies is shown in Table 4.

TABLE 4.—TOTAL WINTER RABBIT CATCH FOR BONE STUDIES

	1945–46	1946–47	Total
Number of tagged rabbits	25*	41	66
Number of untagged rabbits	230	197	427
Total catch	255	238	493
Percent of tagged rabbits recovered	*33*	*26*	

* Includes one road kill and one predator kill.

METHODS OF DETECTING CARTILAGE

To determine if epiphyseal cartilage was present, bones were examined by x-rays and by external features of bones detached from a carcass.

X-ray Test. All tagged cottontails captured in fall and winter were taken to the laboratory for an x-ray examination by Dr. Otto A. Mortensen of the University of Wisconsin Medical School. A foreleg and a hind leg of each animal were x-rayed. In 1945–46 the vertebral column and pelvic region were also x-rayed, but did not yield enough positive information on bone growth to warrant photographing these regions the second year. The exposure technique used was as follows: 50 milliamperes, 40 kilovolt peak, 0.5 second, distance 20 inches, rotating anode, Eastman Ultraspeed film with cardboard holders. Cottontails without tags were not x-rayed.

In an x-ray photograph of humerus or tibia, the presence of cartilage is indicated by a "V"-shaped notch at the proximal end of either bone in the epiphyseal region. The notch appears in the x-ray negative as a dark area extending into the lighter colored bone (Plate 8). It decreases in size as cartilage disappears and an animal approaches maturity. Cottontails showing no notch or other evidence of cartilage are classed as adult by the x-ray test.

X-ray is applicable to both live and dead cottontails. Live cottontails may be x-rayed successfully without the use of a restraining device by holding the animal across its back with one hand and positioning the subject region on the film with the other hand. Care by the handler in avoiding rapid move-

ments and sharp noises will keep the animal quiet.

Bones of dead animals should be x-rayed before removal from the carcass, as detached bones do not always show the cartilage notch clearly.

Groove Test. The simplest means of detecting cartilage, especially in the humerus, is by the presence of a groove or line across the anterior surface and proximal end of the bone in the epiphyseal region (Figure 2). This groove represents the outer edge of the cartilage plate and is the point where final closure takes place. Its presence is best demonstrated by scraping the surface of the bone with a knife to remove all excess connective tissue. If cartilage is present, the periosteum is adherent to it and the bone surface cannot be scraped clean, because the knife edge catches in the edge of the cartilage plate. Cottontails with closed epiphyses show a completely smooth bony surface in the epiphyseal region and no external evidence of cartilage. This method works equally well on fresh or dried bones.

It is recommended that detached bones be stored in a dry condition. Rough cleaning with a pocket knife is the only preparation needed. Dry bones are easier to handle than those kept in preserving solutions, and apparently keep their cartilage-bone color and structural differences indefinitely.

Bones may be examined without being removed from the carcass, if large-scale hunter's bag examinations require speed in handling. An incision in the muscles at the front of the foreleg in the shoulder region will lay the humerus open and make an external cartilage groove visible. This technique does not require removal of any portions of a carcass and there is no loss of meat to the hunter.

It was found, by comparison of x-ray and groove tests on cottontails approaching maturity, that the latter often detected remnants of cartilage that x-ray failed to show. The groove test was therefore adopted as the more accurate. X-ray, of course, is the only method to examine live cottontails, but it requires expensive equipment and can seldom be used in the field. The groove test is faster to use and needs no tool other than a pocket knife.

Other Tests. The presence of cartilage in humerus or tibia may also be shown by making gross sections in the epiphyseal region with a knife, file, or dental saw. Cartilage appears as a thin white line across the sectioned bone surface. It may be identified visually by color contrast with the darker bony area, and by more compact structure when viewed with a binocular microscope. In the late stages of epiphyseal closure, cartilage is difficult to identify in a sectioned bone. Cartilage disappears first at the center of the epiphyseal plate and remains longest at the periphery. Peripheral remnants of cartilage cannot be accurately distinguished from bone without a great deal of practice with this method. An additional disadvantage of sectioning is that bone and bone marrow tend to chip out in cut or filed bones, and thus obscure the visibility of any cartilage present.

Cartilage in very young cottontails can be seen by fluoroscope, but unless used by an expert, this method does not show enough detail in late closure stages to be of use.

Various staining techniques for carti-

lage are available, but were not used in this study, because simpler and quicker methods of showing cartilage were developed.

Disappearance of epiphyseal cartilage does not end the possibility of classifying cottontails for age by bone characters. The pattern of bony trabeculae continues to develop for some time after fusion of the cartilage, but changes are minute and are recognized only with difficulty.

To measure the degree of personal error that might occur when the test is used by persons unfamiliar with it, ten graduate students in wildlife management, without prior experience in bone testing, were asked to classify selected samples of bones for age after a minimum of instruction. Two series of 25 detached humeri whose cartilage condition had previously been determined were used. Bones from tagged cottontails of known age and rabbits of unknown age were included. Students averaged less than one error per series with an average accuracy rating of 97 per cent.

RESULTS OF STUDY

Duration of Cartilage. The initial step in determining the time limits within which the bone test is valid is to ascertain when the first young are born in spring. Earliest litters of cottontails at the Arboretum were probably born about April 15 in the study years. The earliest nest in 1946 was found on April 22 and contained young estimated to be 5 days old. The first pregnant doe of 1946 was trapped on April 6 and carried four well-developed foeti. Study in 1945 was not begun until June, so no indication of the date of first litters was obtained. In both years, young rabbits out of the nest were not seen until the first week in May. Thus the date of epiphyseal closure in April-born young was the limiting date for use of cartilage as an age indicator during the study period.

The age in months of 19 out of 66 tagged cottontails taken in winter could be estimated with reasonable accuracy from weight curves of other known-age cottontails, or was known because they were tagged as nestlings. Open epiphyses were found in the humeri of all cottontails less than nine months of age in the group of 19 rabbits, but epiphyses were closed in those cottontails more than nine months old (Table 5). Bone growth of four tagged cottontails is of special significance. Rabbits no. 11, 26, and A30, born in May and June, and trapped for the last time when $8\frac{1}{2}$ months old, showed only small amounts of cartilage. Rabbit no. 110 was born about April 20 and nine months later had no cartilage in the humerus, but cartilage was present in the tibia, showing that humeral closure was quite recent. These observations indicate that epiphyseal cartilage disappears in the humerus of a young cottontail at the age of approximately nine months. Therefore, when the earliest-born young appear in April, the nine-month period wherein epiphyseal closure progresses to completion ends in January, and January 1 is proposed as the safe terminal date for classifying the age of southern Wisconsin cottontails.

A terminal date in any year is subject to two errors: (1) The birth-date of the earliest litters in the particular year, and (2) a possible error of sampling among the cottontails examined. The

proposed terminal date of January 1 for southern Wisconsin is early enough to minimize these errors. A terminal date also hinges upon the degree of accuracy required. Fifteen of the 16 tagged young of the year shown in Table 5 did not have closed epiphyses before January 15. If this is a valid sample and if 95 per cent accuracy is sufficient, January 15 may be set as a safe terminal date. The latter date was used in classifying the age of cottontails during this study.

TABLE 5.—WINTER CARTILAGE CONDITION OF KNOWN-AGE COTTONTAILS AT TIME OF FINAL CAPTURE

Rabbit Number	First Capture		Est. Birth Date	Final Capture				
	Date	Gram Weight		Date	Gram Weight	Est. age in mos.	Cartilage Condition	
							Humerus	Tibia
20	6/29/45	592	4/20	12/ 2/45	1299	7.5	open	open
110	5/21/46	326	4/20	1/18/47	1224	9	closed	open
101	5/13/46	210	4/25	12/19/46	934	8	open	open
10	6/ 7/45	403	5/1	11/ 7/45	1140	6	open	open
11	6/ 7/45	371	5/5	1/15/46	1122	8.5	open, nearly closed.	open
26	7/ 9/45	541	5/10	2/ 3/46	1304	8.5	open	open
112	6/21/46	400	5/15	11/20/46	1354	6	open	open
16	6/27/45	421	5/20	11/29/45	1098	6	open	open
40	7/26/45	554	5/25	12/ 2/45	1136	6	open	open
23	7/ 7/45	407	6/1	1/11/46	1049	7.5	open	open
30	7/12/45	453	6/5	1/10/46	1185	7	open	open
A30	8/ 1/46	452	6/20	3/ 1/47	1229	8.5	open	open
33	7/17/45	202	6/30	11/ 8/45	869	4	open	open
A24	7/20/46	236	7/1	12/15/46	1090	5.5	open	open
149	9/ 3/46	378	8/1	2/23/47	1082	7	open	open
134	8/25/46	168	8/5	11/28/46	1336	4	open	open
240	Dec./44	?	6/44	1/20/46	1486	19	closed	closed
67	9/14/45	1030	6/45	12/15/46	1415	18	closed	closed
66	9/13/45	1089	6/45	1/25/47	1309	19	closed	closed

Further verification of the terminal date is found in data on young born in late summer and in late-winter age ratios. The per cent of cottontails with open epiphyses in the population decreased sharply after mid-January (Table 6). Since hunting and trapping success remained fairly constant throughout the winter, it seems safe to assume that the decline in number of young classified by the bone test was due to closure of epiphyses of early-born young of the year, rather than to differential mortality or other mechanisms that might reduce the number of young in the population. Summer trapping indicated that last litters were born about the first week in August. The nine-month closure period should end in early May for these cottontails. In 1947 the last cottontail with open epiphyses was found on April 15, although population samples in April and May were small.

It is apparent that earliest spring litters are born at varying times in different years. Thus if the time of birth of first spring litters is known each year, the terminal date for use of the test must be determined each winter by adding 8½ months to the date of birth of first litters.

DISCUSSION

Studies on bone growth have been designed to develop a simple, practical, and accurate method of aging cottontails in the field. Although this end has been met, age ratios compiled with the groove test are possibly subject to unknown distortions. Several questions are as yet unanswered:

What are the cartilage disappearance rates among the different sub-species of *Sylvilagus floridanus*, or in other species of the genus? This paper deals only with the Mearns cottontail (*S. f. mearnsi*).

What are the effects of nutritional deficiencies, disease, or other physiological abnormalities on the rate of bone growth? It is known that poor-soil areas have smaller and fewer cottontails than do good soils (Denny, 1943), and it is possible that the period for the epiphyses of poor-soil cottontails to close is different than for cottontails raised on fertile soils, such as were used in this study.

Will cottontails from other localities in Wisconsin or from other states show the same growth rates as those on the study area? Does length-of-day, as well as age, affect the time of closure? It is possible that a January terminal date can be safely used in most of the north-central states.

Does epiphyseal closure take place at the same age in both sexes and in early as well as late-born young? This was assumed to be so. Data gathered during this study suggested that the assumption was correct, but did not definitely establish it.

TABLE 6.—MONTHLY AGE RATIOS

Period	1945–46		1946–47	
	No. of Rabbits	Per cent of Open Epiphyses	No. of Rabbits	Per cent of Open Epiphyses
11/ 1–11/15	8	*88*	25	*87*
11/16–12/15	76	*78*	41	*80*
12/16– 1/15	96	*74*	55	*78*
1/16– 2/15	65	*57*	39	*54*
2/16– 3/15	3	*33*	58	*48*
3/16– 4/15	3	*0*	18	*11*
4/16– 5/15	4	*0*	2	*0*
Total 1/16– 5/15:	75	*51*	117	*44*

SAMPLE AGE RATIOS

Ratios by Year. All cottontails taken each year from November 1 to January 15 were used to determine the age composition of University of Wisconsin Arboretum cottontails (Table 7). The three-year figure is 79 per cent juveniles.

Yearly cottontail age ratios will reach their highest value when the age composition of a given population has been measured for several years. Consecutive age ratios compiled during the rise and fall of one or more rabbit cycles may shed some light on the causes of cyclic behavior.

The declining percentage of open epiphyses after the terminal date in winter can be used as an indicator of the birth-months of surviving young.

TABLE 7.—YEARLY AGE RATIOS

Year	No. of Rabbits	No. of Young	No. of Old	Per cent of Young	Ratio Young:Old
1944–45*	38	32	6	*84*	5:1
1945–46	180	137	43	*76*	3:1
1946–47	121	98	23	*81*	4:1
Total	339	267	72	*79*	4:1

* Data from Thomsen and Mortensen (1946).

Since nests are hard to find, and the nest sample is apt to be biased, such an indirect determination of birth-months may throw valuable light on breeding phenology. Table 8 presents a sample of such an analysis, but it combines the two winters of this study and hence is not a valid picture of any single breeding season.

An analysis of this type assumes that there has been no differential mortality between population age-groups. It is also evident that large samples are needed to make such calculations statistically valid.

SUMMARY

The epiphyseal cartilage test proposed by Thomsen and Mortensen (1946) for classifying the age of cottontails was found, during two winters, to be valid in southern Wisconsin to January 15 in 12 young of known age. These and four other young cottontails demonstrated that epiphyseal cartilage disappears at about nine months of age. For accurately classifying population samples in this region when first litters are born in April, January 1 is proposed as the limiting date for this test. If 95 per cent accuracy is sufficient, January 15 is proposed as a terminal date. These limits presuppose data of enough volume to exclude sampling error.

If the cottontails examined during this study are a valid sample, an accurate limiting date for any winter in this region may be computed by adding

TABLE 8.—BREEDING HISTORY FROM AGE RATIOS*

Collection Period	No. of Rabbits	Per cent of Open Epiphyses	
Before 1/16	301	78	
		.....	*13%* born in April
1/16–1/31	66	65	
		.....	*18%* born in May
2/ 1–2/28	89	47	
		.....	*30%* born in June
3/ 1–3/31	23	17	
		.....	*8%* born in July
4/ 1–4/30	11	9	
		.....	*9%* born in August
5/ 1–5/31	3	0	
			plus *22%* adults (from first ratio in table)
			Total—*100%* of population

* Data in this table are taken from the total of two winter age ratios, are not accurate measurements of any single year, but are used to demonstrate the method of calculating breeding periods.

8½ months to the date of birth of first spring litters. If a 5 per cent error can be tolerated, nine months may be added.

The presence of a groove on the surface of the humerus, demonstrable in the field by pocket-knife, was found to be a more sensitive test for epiphyseal cartilage than the x-ray test used by Thomsen and Mortensen. Wildlife students without special training applied the groove test with 97 per cent accuracy.

Fall and winter cottontails classified for age by the groove test showed 76 per cent young up to January 15, 1946, and 81 per cent young up to January 15, 1947. The progressive decline in per cent of open epiphyses beyond the limiting date is proposed as a means of estimating birth-months of the surviving young in a winter population.

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BRIEFER ARTICLES

A SCANNING DEVICE, USEFUL IN WILDLIFE WORK

Aerial photography is playing a constantly increasing part in appraising the habitats and censusing the numbers of wildlife. In some directions satisfactory photographic techniques have been developed; in others, much remains to be done. Among the latter is the need for equipment, planes and technique in photographing large numbers of waterfowl, and, even after these objectives have been attained, there is need for a rapid and reasonably accurate method for counting large numbers of individuals on the photographs taken.

Whereas present military cameras, and processing techniques now available, are thoroughly adequate for the taking of satisfactory photographs of waterfowl under favorable conditions, there still remains much to be learned regarding optimum altitudes for the various types of equipment, the development or modification of smaller and slower planes to do a better job, and the training of more expert aerial "duck photographers." In addition, there remains the perfecting of a method or device that will permit the counting on photographs of large numbers of ducks without undue expenditure of time and eye-strain. To attempt to count with reasonable accuracy an irregular raft of 50,000 or more pintails photographed along the Texas coast and recorded on possibly ten or a dozen overlapping K-17 prints is no mean task. Yet things like that have to be done in some manner if aerial photography of waterfowl is to be followed to its logical end. The device described in this article. was devised to facilitate such counting. It may have use in the careful scrutiny of any extensive or confused photographic print. Although it will not remove the demand for time and patience, it will increase the accuracy and reduce the time and effort needed.

The device can best be described by reference to the figures accompanying this article. Its overall appearance (Plate 9, *A*) is that of a shallow box, approximately 13 inches by 11 inches by 2¼ inches in dimensions with a hinged lid (CP) made of 28 gage brass. In this lid there is a curved slot or aperture (SS). The curvature of this slot is the same as that of the route of an 8-power binocular microscope mounted at the end of an arm pivoted on a standard to the right of the "scanner." This slot can best be fabricated first by marking the desired curve on the brass plate, then cutting the plate in two parts along that line with a metal band saw and finally soldering the parts to edge strips of brass, leaving the desired aperture between the two. The width of this slot must be precisely the same as the distance between notches in a milled track on the bottom of the scanning board shown in Plate 9, *C* (TT). In the model figured it is 3/16ths of an inch.

Plate 9, *B*, shows the brass cover plate lifted to reveal the photograph (P) which has been scotch-taped onto the scanning board (SB). The latter moves a specified distance to the right with each depression of the operating lever (OL).

Plate 9, *C*, shows the scanning board removed from its normal position and inverted to reveal the toothed track against which the operating hook (OH, Plate 9, *D*) works. The toothed track was fabricated from a margin control track of a Royal typewriter from which every other tooth was removed. The brass edgings (BE) of the scanning board slide with moderate, smooth friction, in the brass channels (BC) attached to the front and rear edges of the box. Both the edgings of the scanning board and the slots in which they travel consist of "channel brass" which may be obtained in sizes that will slip, one within the other, after a little work with file, emery, and lubricating oil.

Plate 9, *D*, reveals the operating mechanism. The operating lever (OL) when pushed downward activates the operating hook (OH) mounted on a cam (OC) at the far end of the operating shaft (OS), thrusting it to the right. Its forward movement is controlled by the plate (MCP) striking the top of the stop (MCS). The recoil movement of the operating shaft (OS), imparted by the spring (OSS), is arrested by the bottom of the same stop. The operating shaft, as shown, is in the recoiled position. By careful adjustment of the stop controlling the operating lever, the forward thrust and recoil of

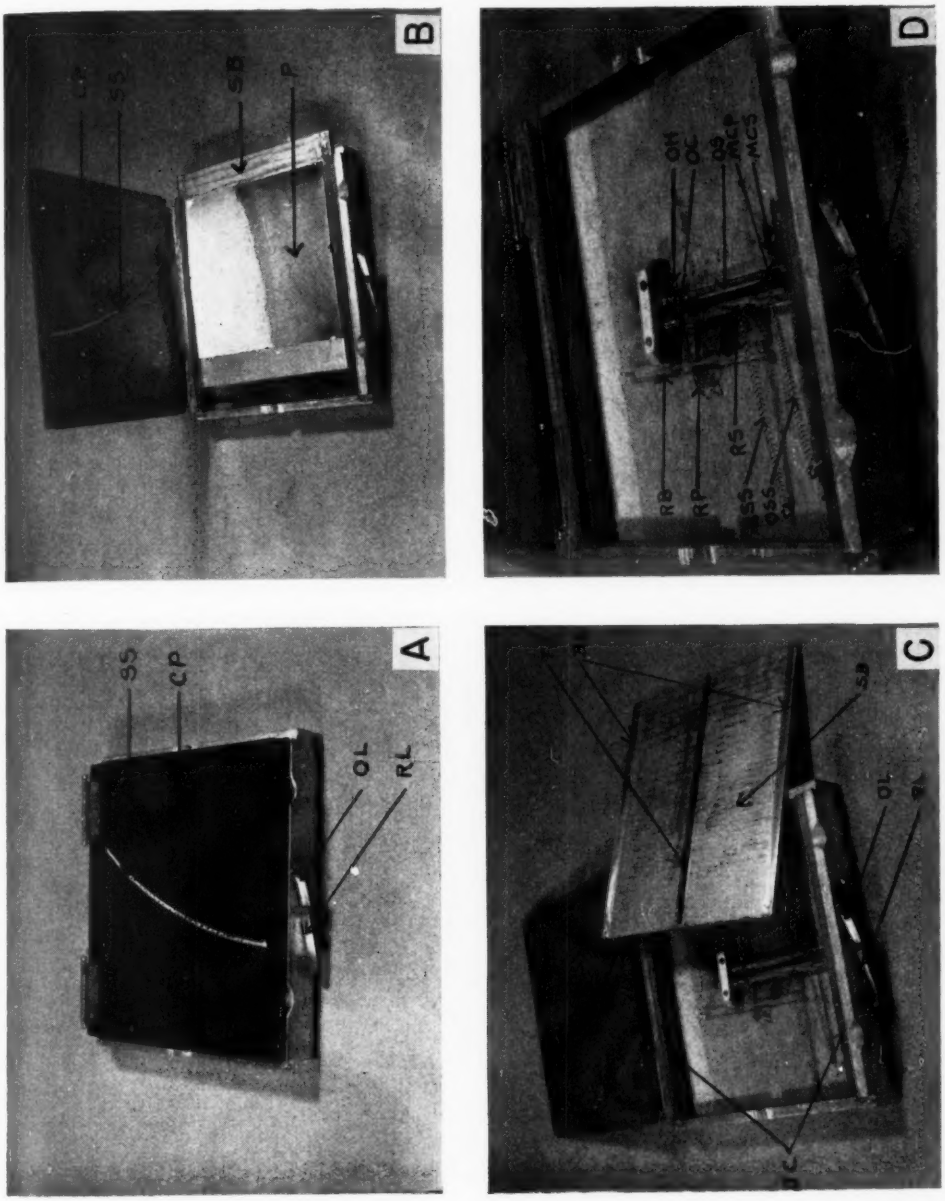

PLATE 9.—*A*. Scanning in position to operate. SS, scanning slot; CP, cover plate; OL, operating lever; RL, release lever. *B*. With cover lifted. CP, cover plate; SS, scanning slot; SB, scanning board; P, photograph. *C*. With scanning board removed and inverted. BE, brass edgings (channel brass); BC, brass channels; TT, toothed track; SB, scanning board; OL, operating lever; RL, release lever. *D*. Operating mechanism. RB, rubber band to depress posterior end of operating hook; RP, release plate, for leveling operating hook; RS, release shaft; RSS, release shaft spring; OSS, operating shaft spring; OH, operating hook; OC, operating cam; OS, operating shaft; MCP, movement control plate; MCS, movement control stop.

the operating hook (OH) can be made to engage successive teeth on the milled track (TT) on the under side of the scanning board (SB). In that manner the forward movement of the scanning board at each trip of the operating lever equals the width of the scanning slot and a new field is placed under the slot for observation.

The other parts appearing in Plate 9, *D*, are a release lever (RL) which, when lifted, raises a brass plate (RP), thus placing the operating hook in horizontal position and permitting the free movement of the scanning board for removal or adjustment in position. A rubber band (RB) stretched over the posterior end of the operating hook keeps its forward end pressed upward against the milled track of the scanning board. The spring (RSS) returns the release lever and its plate to normal position. When operated the scanning board is placed so that its photograph lies somewhat to the left of the scanning slot. The lever is then operated until that part of the photograph to be scanned appears below the slot. The microscope on its travelling arm is then adjusted to cover the slot in its downward sweep.

If a microscope mounted on a revolving arm is not available and scanning is done with a hand lens or one mounted on a tripod, the scanning slot may be a straight perpendicular one which may be constructed by soldering, the correct distance apart, two rectangular sections of the cover plate.

In counting ducks when thousands are involved and the images of individual birds are from 1/100 to 1/150 of an inch in diameter, a tally counter is useful. Through practice groups of 10 can be estimated by the eye, and counts of 10,000 to 20,000 ducks made in that manner within 2% of accuracy and at a rate of 5 per second. Since there usually will be partially hidden images on the left and right sides of the scanning slot, only those on one side or the other are counted to avoid duplication when the scanning board is shifted to the next strip.—E. R. KALMBACH, *Wildlife Research Laboratory, Fish and Wildlife Service, Denver, Colorado.*

NEGATIVE AERIAL PHOTOGRAPHS

To aid in interpreting ground cover and terrain, aerial photographs that are used in field survey work are printed with considerable contrast and with all possible sharpness. Printed dimly, as rather diffused negative images, however, they have proved useful as base maps for plotting dens, cover, and food in a tagging study of the woodchuck.

A Soil Conservation Service print is placed in a baloptican (Spencer Delineoscope) and the image focused in the desired scale on the wall of a darkened room. After the correct placement on the wall is marked, the projector is turned off, and a sheet of 8½ by 11 photostat paper is fastened on the wall with small pieces of cellulose tape. Following exposure, which may be determined in advance by trial and error, using narrow strips of paper, it is developed in any standard developing solution such as Eastman's Dektol. The prints are rinsed, fixed in standard "hypo" solution, washed thoroughly, and dried.

The degree of contrast may be controlled by varying the exposure and development time. In general, under-exposed but fully developed prints will reveal the landmarks essential for accurate mapping, yet will be dim enough to permit addition of the details in pencil or ink. The above method produces a "negative" print, in which wooded areas and shadows are white, while open fields are darker, This appears to be an advantage for our purposes.

Positive prints are most easily produced in the desired scale by rephotographing the original print to obtain a negative on film. An enlargement is then printed on Eastman Kodabromide "A" paper, which—like photostat paper—is very durable and may be folded without damage. Because of the greater accuracy of the lenses, prints made with a camera and enlarger are generally sharper than those made with a baloptican.

If a negative print with sharper detail is desired, it may be made as follows: Place the film negative up-side-down in the enlarger; make the enlarged print, which will be a positive that is reversed from a directional standpoint; then using this reversed

print as a "negative," make a contact print on a second sheet of paper. The final print will then be correct from left to right but will have lights and darks reversed.

The only equipment required for making contact prints is a sheet of glass somewhat larger than the print. Lay the raw paper on a table, emulsion side up; cover with the paper "negative," emulsion side down; and place the sheet of glass over them to assure good contact. Expose by turning on an overhead light.

A baloptican is useful also for drawing a map to scale from an aerial photograph. Focus on a sheet of paper fastened to the wall and trace over the important features with a pencil. If the baloptican cannot be focused to a small enough scale, the lens may be removed from its housing and secured in a temporary extension tube made of heavy cardboard or light sheet metal.—RICHARD F. TRUMP and GEORGE O. HENDRICKSON, *Ames, Iowa.*

A NEW MARKER FOR GAME BIRDS

In the course of research on the breeding behavior of the ringnecked pheasant (*Phasianus torquatus*), it became necessary to devise some method of marking wild birds whereby individuals trapped in the wild during winter could be distinguished from their fellows during the following breeding season.

Experimentation with dyed feathers, plastic tail plaques (Trippensee, R. E. 1941. A new type of bird and mammal marker. Journ. Wildl. Mgt., 5(1): 120–124) and colored leg bands proved these devices unsatisfactory because (1) individuals could not be identified at long range (100–300 yards); (2) The possible color-combination was not large enough; (3) A marker low on the bird's body could not be seen even in low vegetation. In addition to overcoming these obstacles, it was considered that the ideal marker should be as durable as possible, and capable of being affixed to the bird with a minimum of handling.

Figure 1 illustrates a marker that was developed to meet these requirements. It consists of a silver-plated surgical safety-pin (#2 for pheasants) to which are attached two colored tags. The shaft of the safety-pin is inserted through a small pinch of the loose skin at the back of the bird's neck at its junction with the body, and snapped shut. One tag then hangs over each shoulder just in front of the folded wing.

During the search for a brightly colored, waterproof, flexible material from which to make the tags, there was brought to my attention, through the courtesy of the B. F. Goodrich Company, the existence of a rubber film called "Koroseal." This and similar films may be secured very cheaply, in bright solid colors, from many large department stores. In making the tags described below, it has been found that the satisfactory types of film are thick (.005 inches) and very soft rather than stiff. Where a variety of colors is unnecessary, however, some more durable material, such as light leather, would undoubtedly be better.

The following is a description of the tag used on pheasants; for larger or smaller birds the measurements would necessarily be modified. Each tag consists of a body (of one or two colors), a reinforcement and a numeral. The finished tag measures 3½ inches long by 1¼ inches wide and is of double thickness so that the material for a single-color tag would measure 1¼ inches by 7 inches. This is folded in half laterally in manufacture and a ½ inch by ¾ inch reinforcement of heavy rubber (@ .1 inch) thick is inserted at the folded end. The tag is then placed between two sheets of paper and a flat-iron of 250°–350°F. (the proper temperature for ironing silk) is run firmly over the tag and around the reinforcement, fusing the two layers together and to the reinforcement. Two numerals, of some color of rubber film contrasting with the tag, are cut, each 1¼ inches square, and one is fused to each side of the end of the tag distal to the reinforcement.

Since cocks damage their markers by picking to a much greater extent than do hens, it is desirable to make cock markers more durable. This may be accomplished by making each tag ¼ inch wider and ¼ inch longer than described above, and folding this excess along both sides and the distal

end. Fused in place, this folded material forms a border of four thicknesses of film. The area around the rubber reinforcement prove during the observations described below to be the point of greatest structural weakness; a suggested but untested remedy is the addition of an extra thickness or two of film, fused to the tag where the rubber reinforcement is enclosed.

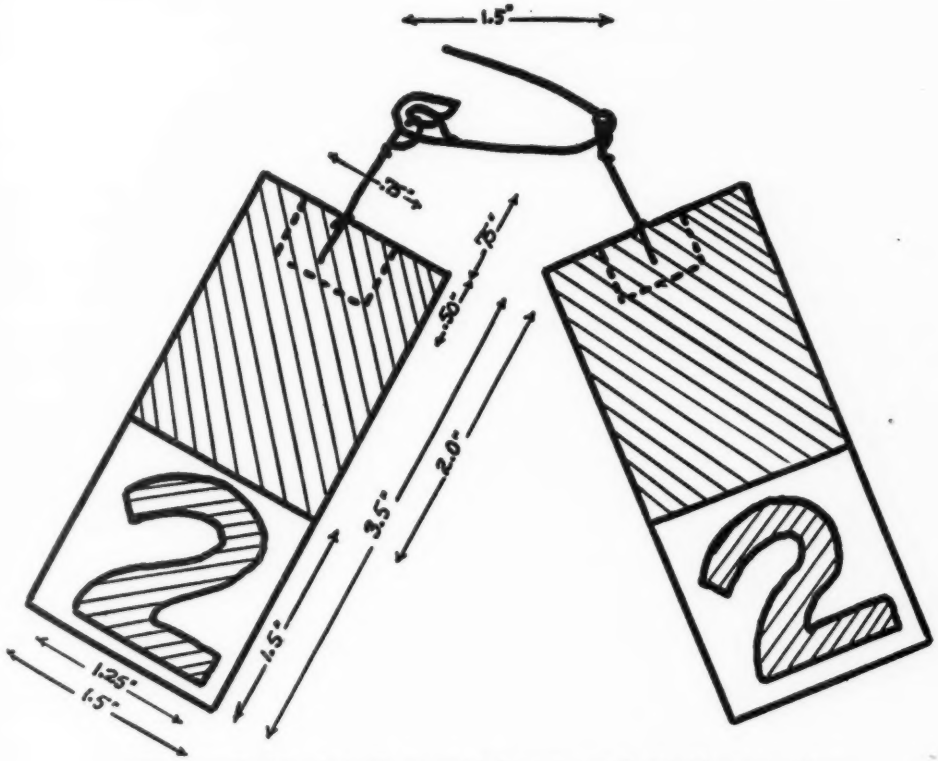

FIG. 1.—Sketch of plastic game bird marker and attaching apparatus.

In case a two-colored tag is desired, the material for the upper (proximal) part and that for the lower are fused together with a ¼ inch overlap, the darker color on the outside. The resultant tag has the same overall measurement as that described above and the numerals are similarly fused to the lower portion.

Next, the reinforcement is pierced near its lower edge, and soft, rust-proof wires about 2 inches long are used to fasten one tag to each end of the safety-pin. The head of the safety-pin must be slightly compressed to prevent the wire loop from slipping along the shaft of the pin. The finished marker, consisting of safety-pin, wires and tags, weighs about five grams.

Howard Twining, former Assistant Game Biologist, Federal Aid Project 22-R, of the California Division of Fish and Game, was sent one of the earlier models of this marker for trial. He subsequently wrote to the author that he had developed a variation of it, in which a length of 20-gauge nickel wire was substituted for the safety-pins and wire fasteners; the second tag was fastened to the end of the wire after it had been thrust through the pinch of skin. This type has not been tested by the author; those markers mentioned below are of the type described in previous paragraphs.

The following conclusions are based upon (1) five months of observation of 25 penned

ringnecked pheasants, marked through permission of the Wisconsin State Conservation Department; (2) five months of observation of over 200 wild ringnecked pheasants trapped and marked during the winter of 1947–48 by the author while in the employ of the Wisconsin State Conservation Department (Federal Aid Project 9-R. Pheasant Management Research); and (3) a verbal communication from Allen W. Stokes, Industrial Fellow, University of Wisconsin, in charge of the Pelee Island Pheasant Demonstration Project concerning tearing of the skin in trapped birds.

Durability. Occasional loss of markers through tearing of skin in birds crowded in a trap may be found when the pin is inserted through a pinch of skin one inch or more wide (Stokes, op. cit.). This loss may be obviated by inserting the pin through a very small pinch of skin ($\frac{1}{4}$ inch to $\frac{1}{2}$ inch wide); the author marked all his birds in this way and found no tearing, presumably because the narrow anchorage allows sufficient "give."

Damage by marked birds to their tags has been mentioned. Using tags which were of only a single thickness of film around the heavy rubber reinforcement, the author found that about thirty per cent of the cocks and a much smaller proportion of the hens had lost their tags five months after marking, largely because of failure at this point; the extra thicknesses of film suggested above would doubtless strengthen this point and lower such losses.

Damage by weather was most marked at temperatures of 0°F. and below. Under these conditions, the tags became stiff and brittle, liable to being torn by vibrations set up during flight, when the fluttering of the tags can be clearly heard as the bird flushes. Those tags made of the heaviest, softest film, and with proper care in attaining perfect welding, withstood short periods at −20°F. with little damage.

Fading, over a period of six months of exposure to sunlight, does not impair field visibility.

Definite conclusions regarding durability can not yet be made. My estimate is that when wild pheasants are marked with rubber-film tags during the winter, about one-third of the cocks and two-thirds of the hens will still retain them by the following fall. If the tags were made of some very tough, flexible material, like leather, the marker would probably last the bird's lifetime.

Series and Visibility. By using four colors (white, red, yellow and blue) and ten numerals (0–9), it has been possible to make a separate series for each of four year-classes (the year class being denoted by the color of the lower square) with 80 combinations in each series. No difficulty in distinguishing color has been encountered in the field.

Under conditions most favorable for observation, it has been found that the greatest range at which these markers can be read is 300 yards (with a 20× telescope).

Effect on the well-being of the birds. Predation upon marked birds has not been measured, but it seems reasonable to assume that they would be more vulnerable than unmarked birds.

A comparison of winter weight-loss rates between marked and unmarked birds was made possible through the kind cooperation of Mr. R. A. McCabe, University of Wisconsin Arboretum Biologist, and Mr. R. S. Ellarson, Graduate Assistant. Of the marked Arboretum pheasants, twelve were retrapped at intervals through the winter. The weight-loss rates of these birds were compared with those of twenty-six unmarked birds of similar trapping history. Statistical analysis of these samples indicates that under the conditions of the experiment, the application of the marker probably causes a sudden, short increase in weight loss rate, which is soon diminished, so that by the end of two months from the time of marking, no weight loss attributable to marking may be detected.

It has also been observed (Taber, MS.) that some marked cocks are successful in establishing territories, while some unmarked cocks are not. This suggests that cocks do not labor under any important psychological handicap because of being marked.

The long-range effects of this marker upon the bird are not yet known, but at the date of writing (May, 1948) an intensive field study of pheasant behavior has revealed no differences between unmarked birds and those which have borne markers for four months or longer.

SUMMARY

In response to the need of marking a large population of wild ringnecked pheasants individually, the author developed a marker consisting of a safety-pin to which are attached two rubber-film tags. The method of making these is described and pertinent conclusions regarding durability, visibility, and effect on the well-being of the bird, based on field observations, are presented.—RICHARD D. TABER, *Department of Wildlife Management, University of Wisconsin, Madison, Wisconsin.*

HATCHING DATES OF QUAIL IN WISCONSIN[1]

The procedure usually followed to obtain information on the period of hatching for any bird is to make a nesting study throughout the period of such activity. A nesting study, however, requires a large corps of field men, is usually limited to a local area, must cover a long period of time, and is often subject to distortion due to nest desertion.

In the present studies the determination of hatching dates for the bobwhite quail (*Colinus virginianus*) is approached by obtaining a random collection of juvenile quail in the fall. The age of the juveniles can be determined by noting the progress of the post-juvenile molt of the primaries (Petrides and Nestler, 1943). Application of the post-juvenile molt in determining hatching dates has been described for several gallinaceous birds by Thompson and Taber (1948).

The theory behind this approach, then, is that a random sample of juvenile quail taken throughout the area under consideration during the fall period will provide a frequency distribution of hatching dates for quail alive during the fall period. Hence the material gathered by this method differs in one important respect from that which would be obtained from a conventional nesting study; it represents only what lives into the fall period. Presumably the first part of a hatching curve derived by this method, as illustrated by Figure 1, may not fully represent early hatches since greater chance for mortality and nonrepresentation in the fall sample may exist for the early-hatched birds.

Certain practical considerations limit the span of the collection period. The beginning date must follow the completion of nesting activities, as collections commenced during such activity would give distortion due to the massing of data referring to the earlier part of the season.

The terminal date for the collection is fixed by the date on which the first completed molt is observed, the age at this time being 150 days in the quail. Normally the juvenile bobwhite terminates the primary molt with dropping and replacement of the eighth primary (A. Starker Leopold, 1939).

For the northern part of the bobwhite's range the "safe" limits of the collection period are probably October 15 to November 15.

Completely randomized material was not obtained in the 1947 collection. Complications arose from closed seasons in the majority of the quail counties, more or less concentration of effort in certain areas, and the greater vulnerability of younger birds to the gun. Further, the collection period was October 1 to December 10 which exceeds the "safe" limits mentioned above. Partial corrections have been made for this and are discussed below.

The collection for 1947 included in Figure 1 was gathered from three sources, namely, solicitation of quail hunters, personal collections, and late fall live-trapping. Each hatching date represents the hatching date of a brood, and material was gathered in such a manner that no possibility exists of the same brood being represented more than once. Wings sent in by quail hunters provided data on 91 of the 156 broods. Since the quail kill in Wisconsin is meager, it is difficult to obtain material by this means. On the other hand the season in 1947 was only five days in length so that it was possible to establish the date of collection with a maximum error of three days; the middle date of

[1] This study was supported by a grant-in-aid from the Wisconsin Alumni Research Foundation and by Wisconsin Pittman-Robertson Project 14-R-1 (1948). J. J. Hickey was kind enough to examine the manuscript.

the hunting season (October 25) was used as the collection date. Brood hatching dates were tallied from the material submitted by any one hunter in a number equal to the maximum number of different ages of birds represented. Any replication of ages (that is, indicated ages differing by less than one week) was assumed to be due to birds being shot from the same brood, and such replications were not tallied.

The personal collections provided data on an additional 49 broods, and the late fall live-trapping provided data on the remaining 16 broods.

Although birds were actually assigned an age in days (Petrides and Nestler, 1943), various inaccuracies make it undesirable to represent the age closer than the nearest week. The histogram in Figure 1 presents the number of broods in the fall collection which hatched in the indicated weekly intervals. The continuous line is the three-week moving average.

Included in the collection are two broods which hatched after October 1 that were caught by hand when a few days old. Such very late birds are not amenable to sampling by the gun in the manner of the strong-flying birds. Further, nine broods that had completed their molt are included in order to take advantage of a large bulk of material obtained up to December 10. It is necessary to include the nine broods to prevent introduction of bias into the sample. Computation of the latest possible hatching dates of these broods showed that they all hatched before June 29; hence the hatching dates of the nine broods were distributed over the first

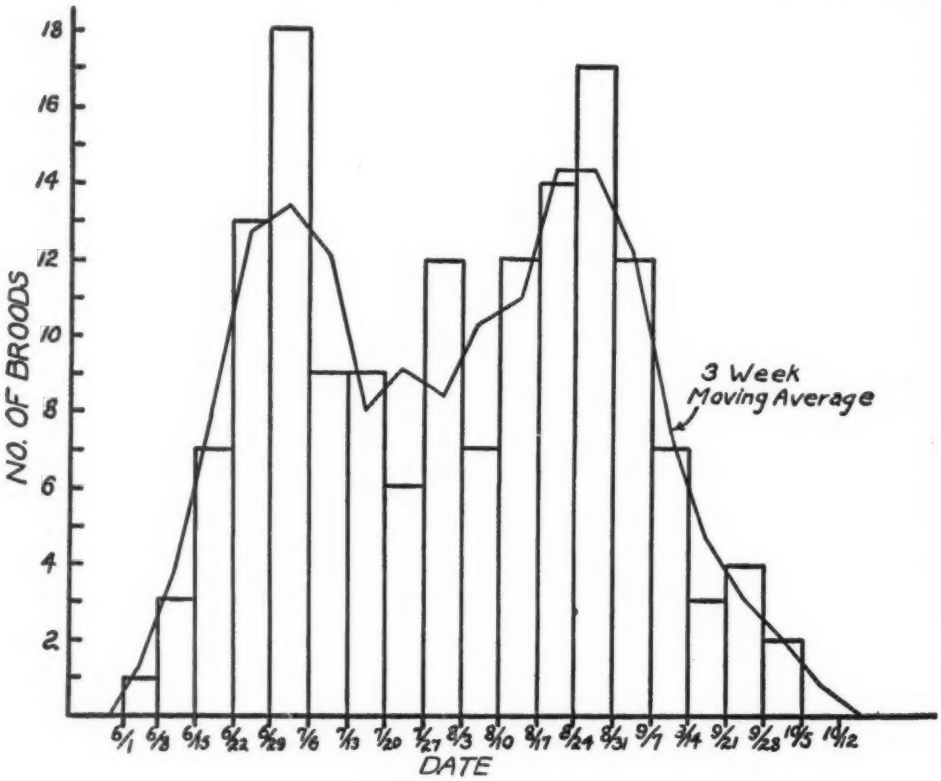

FIG. 1.—Distribution of hatching dates of 156 broods of quail alive in fall, Wisconsin, 1947.

four weeks of the histogram in the proportion in which material was represented for these weeks without the nine broods.

Two peaks are apparent in the hatching curve in Figure 1. A simple test of significance indicates that there is a high improbability that the peaks result from a chance error in sampling. It is important to bear in mind, however, that a truly randomized sample was not obtained as is indicated above. Whether the trough represents a relapse in nesting activities or a period of extra-heavy nest losses or mortality to broods coming off at this time is not known. If a relapse in nesting is the cause of the trough, the second peak would be the result of delayed but successful second nesting. It is also possible that the second peak could have been produced as the result of unsuccessful second nesting efforts followed by highly successful third nesting attempts. Further interpretation and correlation with weather conditions must await repetition of studies in following years to determine the variation to be expected in the distribution of hatching dates.

The graph indicates the limited contribution of the early part of the nesting season to the 1947 fall population in Wisconsin. Half of the broods alive in the fall period hatched after August 1. More broods are represented for the four weeks from August 10 to September 7 than for any other four-week period. Errington (1933) made observations on 31 Wisconsin nests and found that 22 of the clutches hatched before August 1 and 9 hatched after this date.

Kabat has collected data of this type since 1944 in connection with University of Wisconsin studies, but never on a sufficient basis for comparison with the 1947 data. His 1946 material on 22 broods collected on a 10,000 acre area indicated that broods came off from June 1 to the middle of September with one or two broods represented for most of the weeks.

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OBITUARY

PAUL RODE

1901–1948

Paul Rode, Sc.D., Chief of the Museology Department at the National Museum of Natural History, died suddenly in Paris September 23, 1948.

His professional life was spent entirely in Paris. After having taken his degrees in histology and physiology at the Sorbonne, and studied bacteriology at the Pasteur Institute, Paul Rode was first engaged by the Minister of Agriculture and he worked at the Centre National de Recherches Agronomiques and at the Institut National Agronomique between 1927 and 1932. He then passed to the National Museum of Natural History as Assistant in the Mammal Department, where he remained until 1946, when he was appointed Chief of the newly created Service of Museology. In that capacity he was in close touch with curators of all the French Provincial museums of Natural History. He was already closely associated with them, as well as with those of the various art branches, as General Secretary of the Association of Curators of Public Collections.

Although he had published earlier studies on other subjects, Rode had long specialized in Mammalogy. He was the editor of "Mammalia" from its foundation in 1936. Among his most important contributions, the following can be mentioned: Les Mammifères de France; L'Atlas des Mammifères de France; Les Primatés de l'Afrique; Les Ongulés de l'Afrique Noire; Les Singes Anthropoïdes; Les Chauves-Souris de France, and Catalogues des types des Collections de Mammifères du Museum d'Histoire Naturelle.

He was a member of many scientific societies in France and elsewhere, including the Wildlife Society and the American Society of Mammalogists, in this country.

Unassuming and cordial, conscientious and devoted to his duties, he had won the esteem and affection of all those who had crossed his path. For over fifteen years, I have had the privilege to be associated with Paul Rode in various activities, and I was able to appreciate his great technical and personal qualities. His untimely departure has grieved his friends and deprived French science of one of the ablest vertebrate zoologists.—J. DELACOUR.

NEWS NOTE

This number of the Journal of Wildlife Management is the last to appear under the editorial supervision of Harlow B. Mills. Beginning with the July, 1949, number, Dr. Gustav Swanson, Department of Conservation, Fernow Hall, Cornell University, Ithaca, New York, assumes the duties of Journal Editor. The present editor is certain that the cooperation and understanding extended to him during the past years by the members of the Society will continue with Dr. Swanson. All manuscripts, books and papers for review, and correspondence concerning Journal publication should be directed to him.

REVIEW

The Fresh-water Fishes of British Columbia. G. Clifford Carl and W. A. Clemens. British Columbia Provincial Museum, Victoria, B. C. Handbook No. 5. 132 pp., illus. 1948. $0.50.

This is the fifth in the Handbook Series of the Provincial Museum describing the fauna and flora of British Columbia. The booklet is well organized and contains helpful keys and good descriptions of the sixty-three species and sub-species of fishes known to occur in British Columbia. The numerous illustrations, some in color, and glossary should prove useful to sportsmen and others interested in identifying the fishes of this Province. Accompanying the descriptions and distribution of each fish are informative notes pertaining to its habits, game and food qualities, economic importance, and other remarks of interest. Sportsmen and biologists alike interested in British Columbian fishes should find this booklet a worthwhile addition to their libraries.—WILLIAM C. STARRETT.